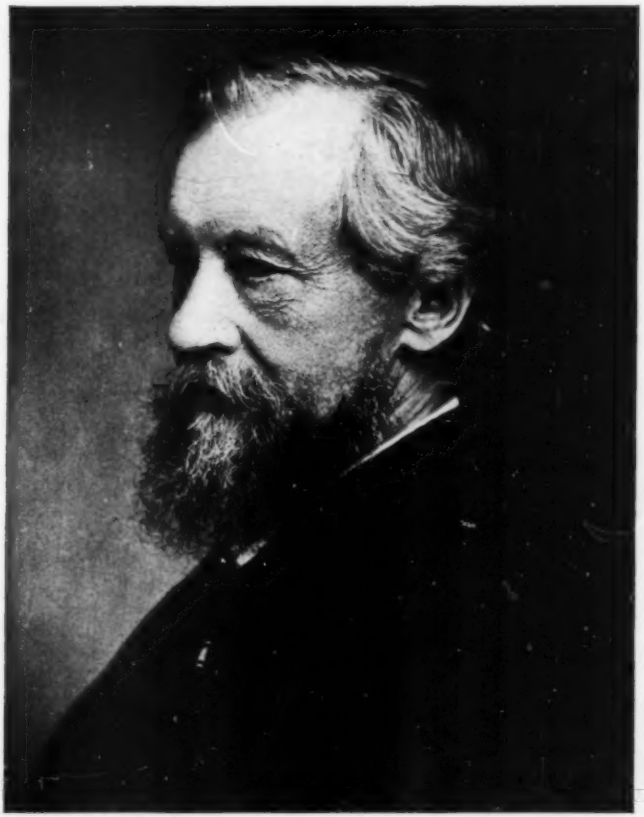
The Journal of HEREDITY



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Hugo de Vries.

Eighty-Fifth Birthday Greetings to Mendel's Rediscoverer and Oenothera's Discoverer

VOLUME 24 JANUARY, 1933 NUMBER 1

The American Genetic Association

An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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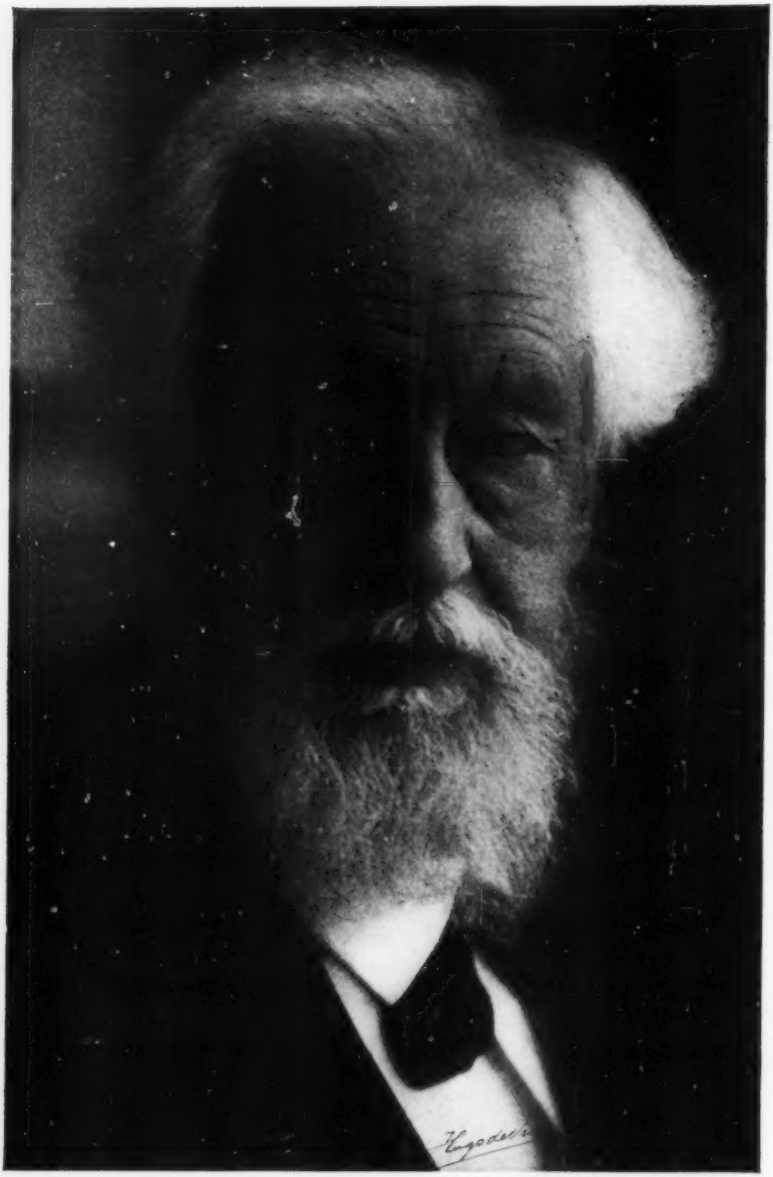


Photograph loaned by Dr. R. E. Cleland

DISCOVERER AND REDISCOVERER

As the dean of rediscoverers of Mendelism and as a discoverer in his own right, the genetic world greets Dr. Hugo de Vries on his eighty-fifth birthday—February 16, 1933.

HUGO DE VRIES AT EIGHTY-FIVE

GENETICISTS have the unique privilege of greeting in this year 1933, on the eighty-fifth anniversary of his birth, the founder of their science, Hugo de Vries (born February 16, 1848), and of extending to him, still very much alive, their hearty felicitations and best wishes for additional years of productiveness in the field which his own penetrating philosophical insight, clever planning, patient and indefatigable industry, and masterly exposition discovered and threw wide-open to his own and subsequent generations of biologists.

His activities and their rich results are too well and generally known to make necessary or to justify at this time a detailed biographical sketch.

After having won great distinction by his discoveries in plant physiology, particularly in relation to osmotic pressures in plant cells, he turned to the problems of organic evolution. He was the first to see clearly the inadequacy of the older methods of attack on these problems, and to recognize that something more was involved than the gradual accumulation of quantitative variations. Recognizing the general occurrence of qualitative differences between species he became convinced that an appropriate technique would enable the observer to actually see the process of evolution going on, and he set out to find organisms adapted to studies of this kind. The evening primroses were only one of many plants which came under his observation, in his search for the most suitable material on which to work.

From the start he recognized a clear distinction between fluctuating variations, which follow the distribution of Quetelet's probability curve, and mutations which represent sudden and specific changes in the genotype, and he saw in the latter alone the fundamental material of evolutionary progress.

The Mutation Theory

Adopting as his distinctive research instrument the strictest kind of pedigree breeding, he accumulated during a period of fifteen years the basic material for his two papers announcing the rediscovery of the Mendelian principles of heredity, published in 1900, and for his big two-volume work on the Mutation Theory, which appeared in 1901 and 1903. During the same years he published many studies on the variation and inheritance of such abnormal characteristics as fasciation, torsion of stems, virescence, doubling of floral parts, the periodicity of partial variations and the relation of feeding to the effectiveness of selection, and in 1899 he published his little book on *Intracellular Pangenesis* in which for the first time the view was presented that the "pangenes" or fundamental units of organization in living beings are duplicated in every cell of the body, a view which is now generally held by all biologists. In the same year 1899 he seconded Correns' interpretation of the phenomenon of xenia as the result of double fertilization, just as Correns the next year seconded de Vries's announcement of Mendelian heredity.

The essential harmony between Mendelism and the Mutation Theory, the simplicy of the methods through which they could be tested and their validity demonstrated, the vast accumulation of supporting data which accompanied their announcement, the suddenness with which these revolutionizing concepts were launched, and the fact that other investigators were on the verge of reporting corresponding results derived from the application of similar methods sufficiently explain the grand impression made on the biological world by these contributions.

There was a sudden rush of investigators to take up the problems thus so effectively brought upon the bio-

ALLIES FOR NEARLY FIFTY YEARS

Dr. de Vries on the occasion of his visit to the University of Chicago in 1904. With him in the photograph is a plant of the species he has done so much to make genetically famous, the evening primrose, (*Oenothera Lamarckiana*). Fifteen years' study of the behavior of this plant (and of other species) formed the ground-work for his announcement of the rediscovery of Mendel's laws in 1900, and of his Mutation Theory of evolution published the following year. The evening primrose has remained a fruitful genetic battle-ground for thirty years and is still holding its own as a source of information regarding the mechanism of variation and evolution. Photograph for Figure 1 and cover illustration loaned by Dr. George H. Shull.

logical stage; and the instant positive, almost wholly confirmatory, results secured by every competent student quickly dissipated the barrage of criticism which any innovation of such far-reaching significance inevitably meets.

To the glory of our great leader be it said that the sudden transformation of his pet province from one of a personal monopoly to one of all but universal possession and active cultivation, led to no such disasters as might have been the result had he been less well poised. Criticism brought neither discouragement nor bitterness; adulation made no visible change in the simple, modest, kindly, lovable friend of every seeker for the truth.

Visits to America

America has every reason for a feeling of satisfaction with the promptness and the cordiality of the response on this side of the Atlantic to the new field of biological investigation and to its discoverer. At the New York Botanical Garden, Doctor D. T. MacDougal began immediately the first confirmatory work in this country. In the summer of 1904 the Carnegie Institution of Washington formally opened its Station for Experimental Evolution, and Hugo de Vries made the address at the opening on June 11, on the subject "Experimental Evolution," this being the first of his many American lectures. He gave later in the same month the Convocation address at the University of Chicago, and then went on to California where he gave an extensive series of lectures at the Summer School of the University of California at Berkeley. The contents of these lectures under the title *Species and Varieties, their Origin by Mutation,* was issued by an American publisher, under the editorship of Doctor MacDougal.

In 1906 on his second visit to America, he again gave a course of lectures in the Summer School at Berkeley, California, and published his small book on *Plant Breeding.* He also lectured on this trip in many American universities. In 1912 he made his final trip to America, when he was invited to make an address at the opening of Rice Institute at Houston, Texas, an honor which he shared with Sir William Ramsay, the great physicist and chemist.

An Active "Retirement"

In 1918, after exactly forty years of service as teacher and investigator in the University of Amsterdam, he retired from that institution and took up his residence in a delightful villa on the edge of the quaint little village of Lunteren, Holland. Here he established for himself at considerable trouble and expense his own private station for experimental evolution which has made possible a continuation of his output of new discoveries which have served to hold the wonder and the admiration of his fellow geneticists in every land. Although far removed from the lines of usual tourist travel, his home has been a Mecca sought out by many of the most distinguished biologists of the world, as well as others less distinguished. All have been charmed by the cordiality of their welcome, as well as by the idyllic setting of the villa in a most enchanting private botanical garden, neither too large nor too small to be an appropriate environment for the retired head of the Hortus Botanicus of Amsterdam. Here amid a profusion of flowers, specimen trees and shrubbery, in a large house equipped with great windows glazed with such perfect glass that even the birds often fail to observe the obstruction, still enjoying the devotion of his charming life-companion, and with one of his two sons and his grandchildren as near neighbors, he has carried on his active scientific productiveness long after the age at which most scientists have closed their records.

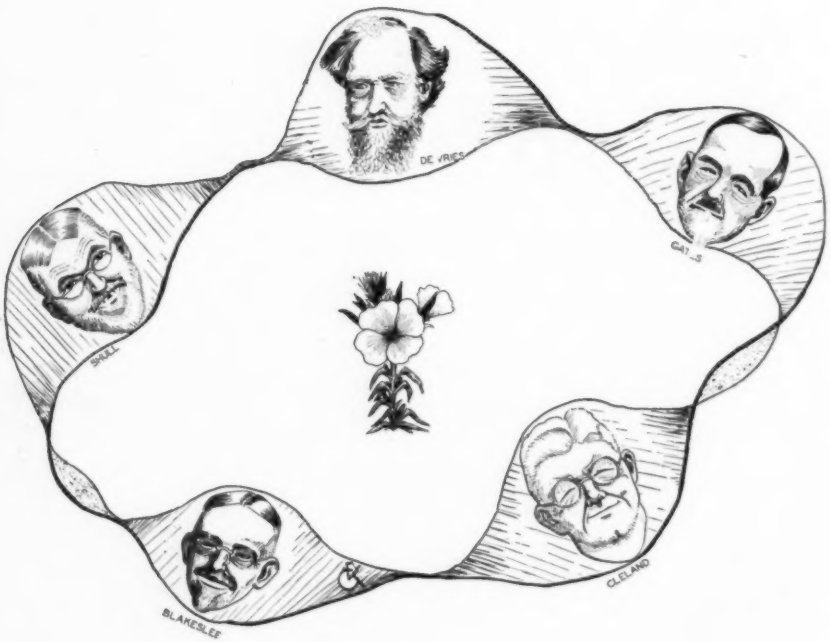
On the occasion of his seventieth birthday, among other activities of recognition, provision was made for the publication of all his journal articles, and these have been continued up to 1925 in seven large volumes comprising over 4,300 pages. In these the later papers have the freshness and

solidity of the earlier ones, and the whole constitutes a vast storehouse of the accumulated results of empirical investigation vigorously presented and adequately discussed.

Who can properly estimate the inspiration to other workers, which has resulted from his noteworthy example of continuous performance and almost unparalleled productiveness during the half century in which he has been actively engaged in genetical research? Something of awe will be mingled with the affection which will find expression in the messages sent to Hugo de Vries by his fellow geneticists on the occasion of his eighty-fifth birthday.

GEORGE H. SHULL.

Princeton, New Jersey.
January 16, 1933.



ARTIFICIAL CULTURE OF SWEET CHERRY EMBRYOS

H. B. TUKEY*
N. Y. State Agricultural Experiment Station, Geneva, N. Y.

IT is characteristic of certain varieties of sweet cherry (*Prunus avium L.*) that they produce no viable seed.[7] Prior to the time of fruit ripening the embryos and endosperm tissue cease developing. The nucellus and integuments subsequently collapse with the result that the seed is characteristically "shrivelled" (Figure 2). Some workers have erroneously interpreted these so-called shrivelled seed as being due to lack of pollination or fertilization. Although fruit may be found occasionally containing no embryo, this situation is rare. Embryos abort or cease development at various stages from about 1 to 5 mm. in length, whereas in a normally viable seed of a late-ripening variety the embryos are nearer 6 mm. in length. Aborted embryos ultimately disintegrate.

It has been shown that this failure to produce viable seed is a feature of varieties of stone fruits which normally ripen their fruit early. Certain varieties of plums (*Prunus domestica L.*) and peaches (*Prunus persica L.*)[1, 6] also behave in this manner.

Because of this situation it has become necessary in the breeding of early-ripening in stone fruits to use as a female parent late-ripening varieties, since the early-ripening sorts do not produce viable seed. This reduces the possibility of securing early-ripening kinds. If embryos of early-ripening kinds could be made to complete their development, it would seem that the chances of obtaining superior early-ripening seedlings would be greatly increased.

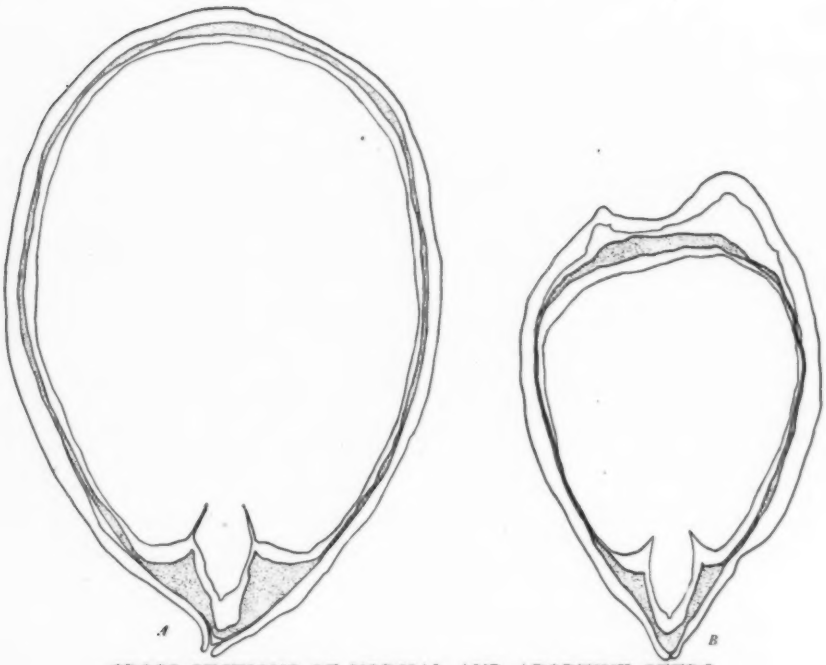
Mature viable cherry seeds must be after-ripened before they will germinate. The optimum conditions are moisture and a temperature of 5 degrees C. for 90 days. Work that has been done with immature seed of other plants[3] indicates, however, that seed of many plants if taken before they are fully mature, will germinate at once. Moreover, in the course of histological studies of cherry seed development, aborted embryos have been found which have developed four pairs of leaves, indicating the possibility of immediate germination and growth under proper nutrient conditions. The problem that has arisen, therefore, is that of artifically culturing these aborting embryos.

Laibach[5] has encountered a somewhat similar problem in Linum, in which embryos likewise failed to develop normally. He suggests the following plan for embryos of this type: "The embryos are to be separated from the mother-plant and put into other conditions before they die on the plant. It would be necessary to undertake premature birth and to observe the fate of the embryos nourished on a fit substratum." Other workers have succeeded in culturing embryos artifically, namely, Hannig[4] using Cruciferae, and Dietrich[2] working successfully with both Cruciferae and Gramineae.

Artificial Culture on Agar

The first attempts were made on nutrient agar, using the early-ripening variety of cherry, Early Purple Guigne. Of many thousands of seed examined from this variety, the author has seen none which were not shrivelled and non-viable, according to the procedure then in use. Later other varieties were tried, namely, Burbank, Governor Wood, and Coe, all of which are classified as early-

*The author is indebted to Dr. Mabel Ruttle-Nebel and to Mr. Alvin W. Hofer for valuable suggestions, and to Mr. K. D. Brase and Mrs. Marion Barrett for assistance.



CROSS SECTIONS OF NORMAL AND ABORTIVE SEEDS

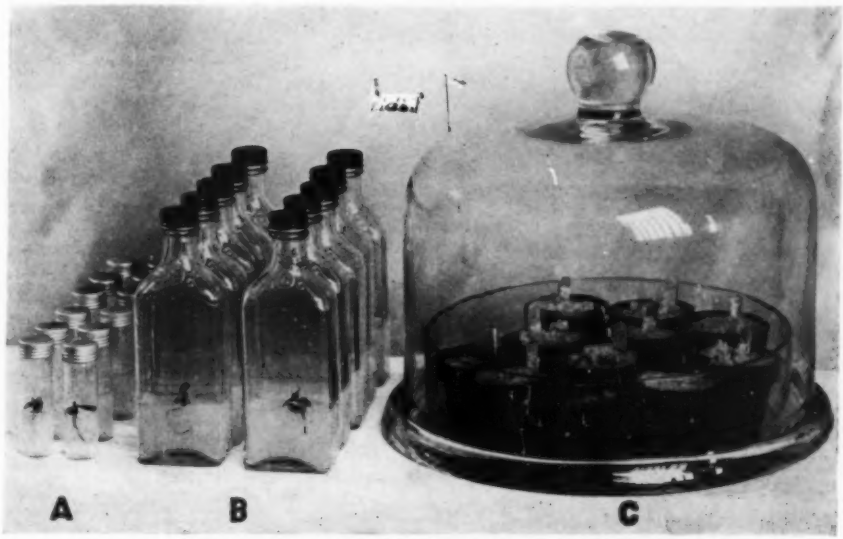
Figure 2

A Viable seed with normal embryo. *B* Shrivelled seed with aborted embryo and collapsed nucellus and integuments. Endosperm is shown as stippled area. X 30.

ripening varieties, and which characteristically do not produce viable seed. The results were essentially the same with all four varieties. For comparison, embryos were taken at the same dates from a late-ripening variety, Downer, which normally produces viable seed.

The procedure was to split the inner or stony pericarp with a scalpel, cut carefully through the integuments, nucellus, and endosperm, and drop the embryo into bottles containing nutrient agar, flaming the mouth of the bottle. Both 4-dram vials and 6-ounce bottles were used, with metal screw top, into which had been introduced 10 cc and 50 cc of nutrient agar, respectively, and all autoclaved for 30 minutes at 15 pounds pressure. (Figure 3.)

In spite of the precautions taken to prevent contamination, approximately 25 per cent of the bottles were contaminated with fungi and bacteria. Although dipping in a solution of calcium hypochlorite helped somewhat, especially in instances where the integuments were not removed, yet contamination continued to be a problem. Best results from the practical viewpoint were secured by sterilizing the bottles and media, placing only one, or at most two, embryos in a bottle, and using a large number of individuals. Although contamination continued to be a factor, the total number of successful cultures was sufficiently large to outweigh losses. With large numbers of embryos per bottle, as 10 to 20, contamination could not be prevented. With smaller numbers of individuals to the bottle, it was possible successfully to free embryos from contamination, wash them in calcium hypochlorite, and place them on



THREE METHODS OF ARTIFICIAL CULTURE

Figure 3

A—Single embryos in 4-drum bottles containing nutrient agar. *B*—Several embryos in 6-ounce bottles containing nutrient agar. *C*—Quartz sand with nutrient solutions. By such means it is possible to produce viable seedlings from varieties that ordinarily are entirely sterile.

fresh media. In this respect the small vials were more satisfactory.

Both Knop's complete nutrient solution and modified Crone's nitrogen-free solution were used, the latter being made up as follows:

KCl—10 g. $CaSO_4$—2½ g. $MgSO_4$—2½ g. $Ca_3(PO_4)_2$—2½ g. $Fe_2(PO_4)_2$—2½ g.	ground together and used 1½ g. to 1 liter of water to which 6½ g. agar has been added.

Agar of this consistency, namely, 6½ g. per liter of water, is sufficiently stiff to support seedlings, and yet not too stiff to prevent root penetration.

During the experiment various other materials were added to the modified Crone's nitrogen-free solution, namely, 2 g. KNO_3, 10 g. glucose, and 2 g. asparagin, per liter.

Embryos were cultured both in the light and in the dark; at room temperature, at 30°C constant temperature, and at controlled fluctuating temperature of 30°C during the day time and 20°C at night.

Results with Embryos Removed

The Early Purple Guigne variety ripens its fruit about 38 days after full bloom. The seed is characteristically non-viable. Embryos were removed from the ripe fruit on June 10, 1932, 26 days after full bloom, and placed on nutrient agar containing neither nitrogen nor a carbohydrate, and kept in direct sunlight in a constant temperature case. In twenty days, the embryos were slightly swollen, but no greening had occurred. They subsequently disintegrated without making growth. A second lot placed in the dark behaved similarly. A third lot placed in the dark and after 16 days supplied with asparagin and placed in the light, also failed to develop chlorophyll and to grow.

A fourth lot, however, containing glucose in the medium and placed in the light developed chlorophyll in the cotyledons within five days, and developed leaves six to ten mm. long and

roots 25 mm. in length within 30 to 35 days. A fifth lot, likewise containing glucose in the medium, but placed in the dark, failed to develop in five days. Upon being placed in the light, however, they showed chlorophyll formation within nine hours, and complete greening of the cotyledons within 23 days.

These results show the importance of a carbohydrate and of sunlight for chlorophyll formation. In fact, the procedure serves strikingly as an elementary plant physiology exercise to demonstrate these points. The cherry seed is a fatty seed, containing 38.71 per cent fat and 28.01 per cent protein when mature, but lacking a carbohydrate.

Chlorophyll appeared first in the edges and tips of the cotyledons, progressing towards the center. The cotyledons increased in size as well as in green coloring, but not necessarily equally. The one most exposed to light became green more rapidly and increased more rapidly in size, in some instances one cotyledon being nearly twice the size of the other. As growth progressed, the primary root appeared, the cotyledons spread apart, followed by rapid development of the stem and the true leaves.

There was a striking difference in the response of the embryos to different nutrient materials. In the case of one lot of Early Purple embryos, amino nitrogen added to the complete nutrient solution plus glucose resulted in large, heavy, dark green cotyledons, but no root development. The cotyledons grew from 4 to 5 mm. in length to 9 to 10 mm., with a very dark green color. Nitrate nitrogen did not produce this effect on a lot run simultaneously. In these, roots developed rapidly and growth proceeded normally.

Although the epicotyl developed in the sunlight in all instances where nutrient solution was complete, in addition to glucose, yet the development of the hypocotyl was not so regular. Root development was more regular in the case of embryos which were removed late in the season. Embryos taken early in the season tended either to be slow in root development or failed entirely.

Results with Embryos Not Removed

The results with Burbank, Coe, and Governor Wood, all early-ripening kinds, were similar. With these varieties, however, attempts were also made to germinate the aborting embryos without removing the endosperm, nucellus, and integuments. Contamination with fungi and bacteria was more frequent, however. In addition, unless the swelling of the embryo by absorption of moisture was sufficient to burst the integuments so as to expose the cotyledons to sunlight, no greening and growth occurred.

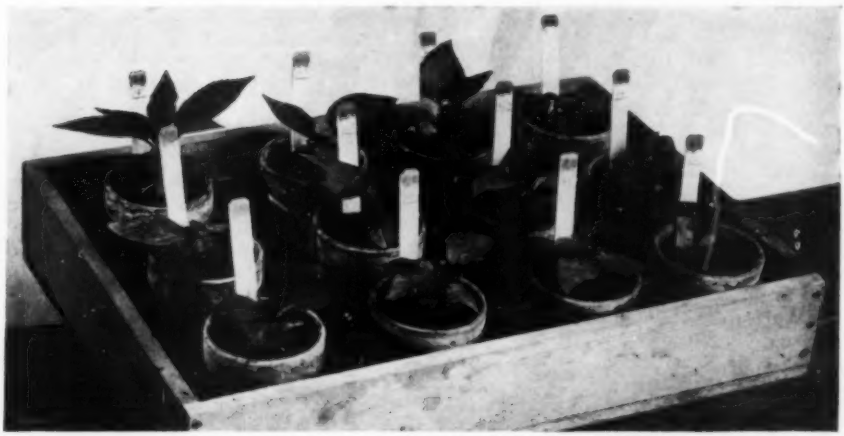
In some tests, the chalazal end of the seed was cut through perpendicularly to the axis so as to cut across the tips of the cotyledons and expose them to sunlight. They developed chlorophyll, grew, and pushed out from the opening thus made in the integuments. The difficulty lay in the fact that the radicle often became curved and twisted due to the chance of becoming encased in the integuments. Yet this method is more rapid than the one in which the embryos are removed, and affords a method for the germination of large numbers, where the loss of a few individuals is not important.

Culture in Quartz Sand

The next step logically was the growing of embryos in sterilized quartz sand under a bell jar (Figure 3). Both the Coe and Governor Wood varieties were used, the seed being taken at the time the fruit was ripe, and at later intervals. Coe ripens 41 days after full bloom and Governor Wood 42.

By this method, small greenhouse pots filled with quartz sand were autoclaved and watered with sterile complete nutrient solution which also contained glucose. The bell jar was wiped with bichloride of mercury, and every effort made to keep the material aseptic.

Seeds were cut through at right angles to the axis at the chalazal end, so as to expose the cotyledons to sunlight. They were then dipped in calcium hypochlorite solution and pressed into the



LIVING SEEDLINGS FROM "STERILE" SEEDS

Figure 4

Seedlings photographed October 10, 1932, grown from aborting embryos removed from cherries during June and July, 1932.

quartz sand with the micropylar end down and the chalazal end of the cotyledons even with the surface of the sand yet exposed to the sunlight. Within five days from the time of planting, the embryos had begun to green and to grow.

Less injury and loss from fungi and bacteria resulted from this method, possibly because of lower humidity under the bell jar than in the vials and bottles.

Seeds containing aborting embryos were also placed on the sand without pressing them into it. While the embryos developed chlorophyll and grew under these conditions, also, yet the radicle often became curved and twisted, resulting in seedlings which were later difficult to transplant.

All seedlings were transplanted to individual pots in the greenhouse when the first pair of true leaves had become well developed. (Figure 4.) Some losses were experienced at this point with damping-off, but no factor appeared different than might be expected with any succulent plant grown under similar conditions.

Dormancy and Germination

As has been stated, cherry seed normally requires four weeks of after-ripening under moist conditions and at a temperature of 5°C. In this connection it is interesting to observe that aborting embryos could be germinated from the time they appeared checked in development, 38 to 43 days after full bloom, until 63 days later, or until disintegration had begun. This is a total of 101 to 106 days after full bloom. On the other hand, embryos of a variety which normally develops viable seed could be germinated readily 42 days after full bloom, only with difficulty 56 days after full bloom, and not at all 67 days after full bloom.

In other words, seed which was aborted never reached the stage of development in which dormancy is involved; whereas seed which is normally viable, finally reached the stage of dormancy. Normally viable seed, however, first passed through a period similar to that of the aborting seed, during which it could be germinated, without after-ripening. The critical period, during the season of 1932 was in the neighborhood of 40 to 50 days after full bloom. Normally viable seed taken at that time germinated immediately but

failed to do so if allowed to develop further.

If dormancy be considered as involving reduction processes, the storage of reduced materials, or a balance involving a high proportion of reduced materials, as contrasted with after-ripening processes involving oxidation and lowering of this balance, then it might be suggested that the balance of materials which bring about dormancy was never reached in the case of aborted embryos. This balance was, moreover, not reached in normally viable seed until 50 days after full bloom. It would seem that here would be a valuable place to study dormancy in seeds.

Practical Considerations

The value of culturing aborting embryos can be seen readily in the case of breeding for early-ripening fruit. With the germination of aborting seed of early-ripening varieties it becomes possible to use these varieties as female parents in crosses in which early-ripening kinds are used as male parents, thus giving a double dose of early-ripening factors. Recommendations until now have been to avoid as female parents those varieties of peaches which ripen the fruit earlier than 90 to 100 days after full bloom[6], and varieties of cherries which ripen the fruit earlier than 50 days after full bloom.

Much time and effort has heretofore been lost by using early-ripening varieties as female parents. Breeding records in which early-ripening varieties have been used as female parents show many fruits procured from the crosses and also show many so-called "seeds"; yet no seedlings. Of course, the difficulty lies in the fact that so-called "seeds" are not seeds at all, but merely the stony pericarp or pit of the fruit, containing within them the shrivelled seeds which disintegrate during after-ripening processes.

What Constitutes Sterility?

The question of sterility is raised by these data. So long as the early-ripening varieties of cherry produced no seed which normally germinated, these varieties were designated as "sterile," "partially sterile," and so on. Now that this sterility is shown to be a matter of nutrition and cultural conditions, can these varieties longer be called sterile? They are certainly not sterile when by artificial manipulation the embryos can be made to develop into seedlings with root, stem, and leaf; yet from the standpoint of viable seed production they are normally considered sterile.

A clear distinction must, therefore, be made between plants which do not produce viable seed because of some genetically lethal factor involved in the gametes or the zygote, and between plants which do not produce viable seed because of some somatic relation which influences adversely the development of the embryo and of viable seed.

Literature Cited

1. Blake, M. A. Growth of fruits of the peach. *N. J. Agric. Exp. Sta. Ann. Rpt.* 4:32. 1919.

2. Dietrich, K. Ueber Kultur von Embryonen auserhalb des Samens. *Flora*, 17. 1924.

3. Goff, E. S. The effects of continued use of immature seed. *Wis. Agric. Exp. Sta. Ann. Rpt.* 17:295. 1900.

4. Hannig, E. Zur Physiologie pflanzlichen Embryonen. *Bot. Zeitung* 62:45-81. 1904.

5. Laibach, F. Ectogenesis in plants. *Jour. Hered.* 20:201-208. 1929.

6. Sakaguchi, I. Relation between maturation of fruit flesh and development of seeds in peach. *Proc. Crop. Sci. Soc. Japan* 2:No. 2, 96-103. July, 1930.

7. Tukey, H. B. The viability of seed from certain cherry varieties. *Proc. Amer. Soc. Hort. Sci.* 1927:129. 1928.

DEAFNESS AS A EUGENICAL PROBLEM

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Types of Deafness

DEAFNESS is of three main types, besides minor disorders such as otitis media and a few types not well understood. The eugenical significance of these types is distinct.

The first type is adventitious or acquired deafness, resulting from misfortune or disease, not as an inheritance from ancestors, and usually arises after birth. Considerable discernment is necessary to determine who should be included in this class, since parents often have not observed carefully. If deafness has been noticed during the years when it is hard to detect, the first three years, and there are deaf relatives, we are safe in assuming that the type is not adventitious but hereditary. Exceptions may be made where the child is known to have had some disease that often causes deafness.

Adventitious deafness is an acquired character in the genetic sense. Such a character is a structure or change that not only develops after the embryo is formed, but which is the result of the environment, of use or of disuse. Diseases and accidents are occasioned by the environment. The evidence for the inheritance of acquired characters has been sifted thoroughly and none of it has been able to stand this scrutiny. Therefore if one is sure his deafness is adventitious he is no more likely to have deaf children than one chosen at random from the population.

The second type of deafness is the hereditary type of deaf-mutism. As indicated above, the criteria for distinguishing this type are inability to hear from early childhood, and the possession of deaf relatives. I agree with Bell[2] and Fay[7] that the latter is the better criterion.

Both adventitiously and hereditarily deaf persons are called deaf-mutes if the affliction arises early enough and is severe enough to interfere with their learning oral speech. If such a child is given a special course in lip reading and speech, it can speak. But the term deaf-mute is well established and is useful in distinguishing among classes of people who have hearing difficulties.

The third type of deafness is called otosclerosis, sometimes miscalled old-age deafness or dry catarrh. This affliction begins very rarely before puberty, more often in middle life, comes on gradually, and usually does not destroy the hearing entirely, though sometimes it does. Its mode of inheritance and the changes it causes in the ear will be discussed later.

Loss of hearing is of various degrees. The term deaf has been used to apply to those whose loss is great enough that they can not profit by oral instruction.

Methods of Investigation

The American Medical Association very kindly made a grant of fifty dollars for a trip to the Volta Bureau, Washington, D. C. This institution is a clearing house for work on deafness, and the conferences there were very helpful. The Bureau's extensive library afforded some excellent data.

The Ohio State School for the Deaf opened their records for family history study, and both this school and the Columbus Day School for the

* Summary of a study of the inheritance of deafness undertaken at Ohio State University. Expenses of the research were borne in part by the American Medical Association.

Deaf furnished addresses of deaf persons. Many of the following data were obtained by visiting families of the deaf in Columbus. A mastery of the rudiments of the sign language aided in gaining the confidence of the people.

Certain types of persons were tested on the 2A audiometer.[1] This instrument makes tones of definite pitch ranging from 64 to 13004 vibrations per second. The intensity is measured in hearing units from 0 to 100. A person who hears these tones below 10 hearing units of intensity has no appreciable loss. These tests were given by the instructors and assistants in the Phonetics Department of Ohio State University. The arrangements were made and transportation furnished by the author. All but two families were tested in sound resistant booths. These two were tested in homes which were very quiet, in the suburbs.

Most of the family histories of otosclerosis were obtained from fellow students, and are their own families. Some are very complete and definite, making one of them worth more than ten sketchy or doubtful cases.

Deafmutism, A Hereditary Defect

Deafness runs in a number of families. Turner,[18] Love,[12] Fay,[7] and Mygind[13] all give some complete family histories. A prosperous family in Missouri is described by Dow and Poynter[5] in which deaf-mutism is traced through four generations. Eighteen persons, all males, 22.5 per cent of all male descendents, were born deaf. However other family histories show only a slightly greater percentage of deaf males than deaf females.

From the records of the Ohio State School for the Deaf the author listed without selection 31 families in which both parents are deaf and at least one child is in the school. The total number of children (excluding two not reported as to hearing) is 89; deaf among these 63, or 70.8 per cent.

Environment, the only alternative to heredity, can not account for more than half of the cases of deaf-mutism. Mygind[13] mentions a pair of fraternal twins, one born deaf and the other hearing. Another pair has come under my observation: boys seventeen months old, one born deaf, hair curly; the other hears, hair straight, 2½ pounds heavier than his brother. An older sister is deaf. Environment can not account for this difference; heredity can. It is significant that no identical twins have been reported of which one was congenitally deaf, the other hearing.

We see from the above that deaf-mutism is much more frequent in families of the deaf than in the general population, it runs in families just like traits known to be hereditary, causing children to resemble parents closely, and that an environmental explanation is inadequate. Doubts should be entertained no longer as to the hereditary nature of deaf-mutism.

However since some hereditarily deaf parents have hearing children, two-thirds according to Fay,[7] and the trait has been shown to be recessive, it can not be transmitted by a single pair of genes. Mrs. Julia Jaster Kraatz[11] has concluded that two pairs of genes are involved.

I have examined the reports of thirty-four autopsies by reliable physicians, mostly by the illustrious Austrian, Dr. Politzer.[15] Below are listed all the cases where the inner ear is described:

	Persons
A. Cochlea absent totally or partially	10
B. 8th nerve absent or small	7
C. Combination of A and B	4
D. Large division of brain wanting, feeble minded also	1

This table suggests that one pair of genes controls development of the cochlea, the other, development of the eighth nerve. This hypothesis should suggest a line of investigation.

Politzer's autopsies suggest further that there is a third pair of genes

that controls development of the middle ear. It is noteworthy that each of the three parts has a distinct embryological origin. We are not so much interested in the third pair of genes, since according to Shambaugh,[16] defects in the middle or outer ear are not sufficient to cause deafness.

There may be many more genes than the above involved in ear development; but we have no evidence that others have mutated.

Audiometer Tests

A. To Distinguish the Genes

Dr. Lawrence H. Snyder of Ohio State University desired that I find some criterion to distinguish the two types of hereditary deaf-mutism. Assuming with Mrs. Kraatz[11] that hereditary deaf-mutism is due to two pairs of recessive genes, and knowing that audiometer records sometimes showed a hearing in the lower register only, and sometimes in the upper register only, he suggested that those having one pair of genes might be able to hear high notes, while those possessing the other pair could hear low notes when tested on the audiometer.

This was a valuable suggestion. If positive results were obtained, deaf persons could be advised whom they could marry with safety. If negative, a fact would be established none the less, and the time of other workers would be saved.

A father and mother who are hereditarily deaf, but whose children can hear, must be possessors of the opposite pairs of genes for hearing. If we designate the genes for normal hearing by letters *BB* and *EE*, one parent in such families is *BBee*; the other, *bbEE*; and the children, *BbEe*. The first parent is deaf because of the lack of the gene *E*, the second because of lacking the gene *B*, both of which are necessary for inner ear development. On the other hand since the children can hear they must have one of each of these pairs of genes.

Accordingly parents of this type were sought, visited, and their statements about themselves checked by inquiring of others. Then their hearing was tested on the 2A audiometer. The table below gives the results:

TABLE I.—Tone-Sensitvility of Deaf Parents of Non-Deaf Children

desig-nation	hearing of relatives; when deafness appeared	highest and lowest notes right ear	highest and lowest notes left ear	remarks
A	brother deaf	128-8192	128-2048	2 children hearing.
A¹	sister deaf; A¹ born deaf	512-1024	1024	wife of A; same children.
B	brother and niece deaf; B born deaf	0	256-1024	1 son hearing very good.
B¹	2 sisters and cousin deaf; B¹ born deaf	512-1024	1024	wife of B; same child.
C	parents and aunt deaf; C born deaf	0	1024	1 daughter hearing; 1 deaf.
C¹	sister deaf	0	0	wife of C; same children.
D	brother and sister deaf	64-4096	512	daughter hearing; son partial.

The results in the above table are negative; there is no tendency for one parent to hear high notes, and the companion, low notes. The note heard most frequently, viz. nine times, was the pitch 1024; next was the pitch 512, heard eight times. The latter is a note of medium pitch. Low notes were not frequently heard.

It is suggested that autopsies of the relatives of the deaf may reveal defects that will indicate what genes for hearing a given person possesses. There are, however, a number of practical difficulties in the way of a very extensive application of this branch of research in human genetics.

B. To Determine Degree of Dominance

That deafness is recessive to normal hearing there can be no doubt. If it were dominant it could not skip even a single generation and make its appearance in the next. Furthermore the dominance of the genes for hearing seems to be complete. Audiometer tests show that persons who are heterozygous for deafness have no defect in hearing provided they have one of each pair of genes for hearing.

A person having no more than ten per cent loss is considered normal. Note that in the following table* no one has more than this amount of loss in both ears.

Otosclerosis

This form of deafness is due to changes which gradually take place in the inner ear. The normal layer of bone of the bony labyrinth is replaced by spongy bone. If this occurs in the region of the oval window, between the middle and innner ears, this space becomes filled with bone. Consequently the base of the stapes is ankylosed firmly, interfering with the conduction of sound waves.

Tonybee and Politzer[6] found a high degree of correlation between loss of function in the ear during life, and pathological anatomy as revealed by autopsy. They have proved that these

*TABLE II.—Hearing of Heterozygous Persons

desig-nation	hearing of relatives	range of pitch; vibrations per second	highest and lowest per cent loss, right ear	highest and lowest per cent loss, left ear
E	parents born deaf, both having deaf relatives	64-8192	15-0	10-0
F	parents deaf-ened young, both having d. relatives	64-8192	10-0	5-0
F_1	daughter of F; father hears	64-8192	10-0	10-0
F_2	son of F	64-8192	0-0	10-0
F_3	daughter of F	64-8192	10-0	15-0
G	two children born deaf	64-8192	5-0	5-0
G^1	wife of G; same children	64-8192	5-0	5-0
H	mother of four deaf children	64-8192	15-0	10-0
I	father of cong. deaf girl	64-8192	15-0	5-0
I^1	wife of I; same daughter	64-8192	15-0	10-0

E. Tested in quiet home; loss greater than 10% in only one pitch, 8192.
F_2. Loss greater than 5% in only one pitch, 512; ear infection, swimming.
G. Loss up to 70% above 4096; blow over eye, scar, abscess.
H. Loss greater than 10% in only one pitch, 4096.
I. Measles.

changes actually are responsible for the deafness.

Kerrison,[10] supported by Politzer[15] and Frey,[8] says that uncomplicated otosclerosis is easy to diagnose. The symptoms follow: progressive deafness, tympanic membrane normal, Eustachian tube permeable during catheterization, Rinne's test negative, low tones inaudible, perception of highest tones still present, subjective noises sometimes. It usually begins in middle life, very rarely before puberty.

Charles E. Perkins[14] states that no cause is known for otosclerosis except heredity; yet there are cases in which the closest questioning fails to obtain any history of the occurrence of deafness in any member of the family near or remote. If this be true the possibility of dominance is barred; it must be recessive.

Gradenigo[9] of Italy decided otosclerosis is recessive, having studied five hundred cases.

Davenport[4] reports seven families in which both father and mother were somewhat deaf. There were twenty-five children, four of whom were less than 13 years old. Of the remaining twenty-one, twenty had hearing troubles. The exception was a man who died at the age of 63, and was not markedly deaf, if at all. But Davenport was not sure this particular family had otosclerosis rather than some other type of ear malady.

In the original dissertation on file at Ohio State University the author gives family history charts for thirty-eight cases of otosclerosis, along with fourteen cases of an unnamed defect. Of the former there are sixteen men, nineteen women, three sex unknown. This disproportion is in the wrong direction to suggest sex linkage. There are nine instances where an otosclerotic person is descended from parents both of whom have normal hearing. A larger proportion of the offspring are afflicted with this defect in families where it is found, than suffer from deafness in families of deaf-mutism. This suggests one pair of genes rather than two.

The hypothesis of a single pair of recessive genes is sufficient to account for all the data that I have seen, either in my own work or that of others. A careful diagnosis excludes some cases and so simplifies the problem.

Summary and Conclusions

This is a study of the methods of inheritance of types of deafness, to serve as a basis for reducing the number of deaf persons in the future.

Deafness was the first trait to be studied from the standpoint of scientific eugenics. The history reveals that the vast majority of deaf people were uneducated and unmarried up to 1840.[15] Since that time they have been segregated for education, most of them marry, and the majority choose deaf partners.

Among the types of deafness we find (a) adventitious deafness, resulting from diseases and accidents and causing mutism if its onset is in a young child; (b) hereditary deaf-mutism, the criteria for which are appearance at birth and possession of deaf relatives; (c) otosclerosis, resulting from ankylosis of the stapes, starting in middle life and progressing; (d) a few minor ailments, mostly not involving the inner ear nor causing total deafness.

That hereditary deaf-mutism and otosclerosis are indeed inherited is proved by the study of family histories and identical and fraternal twins, just as other traits are studied.

Deaf-mutism seems to be transmitted by two pairs of recessive genes. Evidence from autopsies suggests that one of these pairs controls development of the ectodermal part of the cochlea, the other pair, the auditory nerve and its ganglion. Another pair controlling development of the middle and outer ear is likewise suggested. Since persons who are heterozygous can hear perfectly on the audiometer, the trait is complete-

ly recessive. Data on otosclerosis may be explained fully on the basis of a single pair of recessive genes.

Many deaf persons have shown a desire to make the proper choice in marriage,[7] so that their children can hear. If such a one marries a hearing partner who has no deaf relatives, or a person adventitiously deaf who is without deaf relatives, the danger of deaf offspring is slight. When persons who are hereditarily deaf choose partners like themselves, one-third of the unions produce deaf offspring. This suggests that there are certain types of the hereditarily deaf who may marry with safety. However audiometer tests have failed to reveal any criteria for distinguishing them.

In order to promote marriages between deaf and hearing persons, which are desirable if the deaf marry at all, we should stop segregating the deaf. We should increase our day schools, teach lip reading and oral speech, and thus avoid taking deaf persons out of their normal environment.

Literature Cited

1. Abernathy, Edw. R. A tone-intensity comparison of the hearing of deaf brothers and sisters; Thesis (M A) Ohio State Univ., 1928.
2. Bell, Alexander Graham. A few thoughts concerning eugenics; *Nat. Geographic Mag.*, Feb., 1908.
3. ————————. Upon the formation of a deaf variety of the human race; Nat. Academy of Sciences, Washington, *fourth memoir*, 1884.
4. Davenport, Chas. B. Hearing in children; Trans. of Am. Laryngological, Rhinological and Otological Soc., 1930.
5. Dow, G. S. and Poynter, C. I. Dar family; *Eugenical News*, vol. XV, p. 128, 1930.
6. Duel, Arthur B., editor. Otosclerosis, Vols. I and II; New York, Paul B. Hoeber, 1928.
7. Fay, Edw. A. Marriages of the deaf in America; Washington, Gibson Bros., 1898.
8. Frey. The demonstration of two cases; *trans. fr. Monatschrift fur Ohrenheilkunde*, bund 44, s. 1277-1280, 1910.
9. Gradenigo, G. Sordita profunda e sordomutismo in seguito ad otite media non purulenta; Italy. Pamphlets on the education of the deaf, vol. I; on file at Volta Bureau, Washington.
10. Kerrison. Philip D. Diseases of the ear; Phila. and London, J. B. Lippincott Co., 1930.
11. Kraatz, Julia Jaster. A study of the Mendelian factors in the inheritance of deaf-mutism; *Jour. of Heredity*, Vol. 16, No. 7, 1925.
12. Love, Jas. Kerr and Addison, W. H. Deaf-mutism; Glasgow, Jas. MacLehose & Sons, 1896.
13. Mygind, Holger. Deaf-mutism, English edition; London, F. B. Rebman, 1894.
14. Perkins, Chas. E. Manual of Otology; Phila., Lea & Febinger, 1916.
15. Ballin, M. J. Politzer's textbook of the diseases of the ear, sixth edition; Phila., Lea & Febinger, 1926.
16. Skambaugh et al. Deafness; *Archives of Otolarynology*, vol. 7, p. 424 ff. 1928; also vol. 12, p. 190 ff. 1930.
17. Tonybee, Joseph. Diseases of hte ear; Phila., Blanchard & Lea, 1860.
18. Turner, Rev. W. W. Hereditary deafness. *Proc. of First National Conference of Principals of Deaf Schools*, pp. 91-96. On file at Volta Bureau, Washington, 1868.

Sex Linkage in Ducks

Professor R. C. Punnett in *Journal of Genetics*, Volume 25, No. 2. finds sex linkage in crosses of Mallard ducks with the Indian Runner. In F_1 the male ducklings are uniformly darker than the females when the Mallard is the female parent. In the reciprocal cross the ducklings all resemble the Mallard. The broodiness and the flying instinct of the Mallard are dominant in F_1.

INBREEDING AND THE GENETIC HISTORY OF THE RAMBOUILLET SHEEP IN AMERICA*

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History of the Breed

IN the latter part of the 18th century, Spain had a monopoly on the production of fine wool. The product was sold to other countries only because the Spanish factories were unable to utilize the entire output. Fearing that Spain would increase her factories and prohibit the exportation of wool, as she had already prohibited the exportation of Merino sheep, the rulers of France sought to improve the French sheep so that France would be independent of Spain for its supply of fine wool. In 1785 a request was made to the King of Spain in the name of Louis XVI for a grant of Spanish Merinos, for the experimental farm recently established on an estate at Rambouillet near Paris. This request was granted and in 1786 there were brought to Rambouillet 318 ewes and 41 rams selected from among flocks near Segovia in Spain. A second large importation from Spain to France was made in 1801 and a few of these were added to the original flock at Rambouillet. No new blood has been added to the flock at Rambouillet since 1801. Records of the flock have been kept without interruption since 1786.‡

Several of the privately owned flocks of France were founded on stock purchased at Rambouillet and it is said that a few, even today, trace in all lines to the Government flock. However, Spanish Merinos had been brought into France before the importations which founded the flock at Rambouillet. Later during the rule of Napoleon a great many Spanish Merinos were driven into France and undoubtedly many French flocks were formed with these as a foundation on which rams from the fold at Rambouillet were often used.

Spanish Merinos had been introduced into Germany as early as 1765. A number of German breeders, including von Homeyer in the sixties of the next century, obtained stock at the National Fold at Rambouillet and also from other French breeders. With this stock they improved their sheep which later became famous for their size and fleece. Nearly half (as will be shown later) of the ancestral lines traced back from the pedigrees of the American Rambouillets end in foundation animals which were bred in the von Homeyer flock, and a few more lines end in foundation animals from other German flocks. Since we

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‡For details of this early history see: Bernardin's "La Bergerie de Rambouillet et les Merinos," published about 1890. Volume I of the American Rambouillet Record contains a free translation of a Spanish translation of this manuscript but, because of the successive free translations and the summarizing of passages, this English version is not in all respects a reliable original source.

do not know how important Rambouillet-bred animals were in the development of the German flocks, it is probably impossible at this date to make a trustworthy estimate of how much blood, other than that which came through Rambouillet at some time or other, came into the American Rambouillet Record in the foundation sheep. Even that blood which did not come through Rambouillet seems to have been nearly all Spanish in its origin, for most of the other stock mentioned in the old discussions of purity are the Spanish Merinos brought into France in Napoleonic times, and the Spanish Negretti and Saxony Merino ewes which seem to have furnished at least part of the original foundation stock for many of the German flocks.

The Importation to America

The first importation into the United States was in 1840 and came from Rambouillet. A number of importations from the flock at Rambouillet and from other French breeders were made during the next twenty years. Very few were imported during the two decades from 1860 to 1880.

In 1880 von Homeyer sent a ram and two ewes as a gift to W. G. Markham, a breeder in New York. The size and merit of these sheep attracted the attention of breeders and during the next five years several small importations were made. At the World's Fair in Chicago in 1893 von Homeyer had an exhibit of sheep which attracted much attention because of their size and fleece. In all about 70 sheep of von Homeyer's breeding were brought into this country. So enthusiastic were some breeders about von Homeyer sheep that at one time a "von Homeyer Club" was organized among breeders in Michigan and neighboring states. During the ten years following the Columbian Exposition a number of importations were made from German as well as French flocks. Few if any Rambouillet sheep born later than 1904 have been imported to America.

The term Rambouillet as applied to the breed did not come into general use until about 1889 or 1890. The term "French-Merinos" was applied to sheep from France, and "Rambouillet-Merinos" evidently only to sheep from the National Fold. The Rambouillet breeders in America organized in 1889 and published the first volume of the Record in 1891.

The breeding systems which have been followed in this breed are a matter of special interest because importations have ceased for so long and seem unlikely to be renewed. Moreover the Rambouillet is one of the leading breeds of sheep in America and possesses several features of special interest. For example, its centers of breeding are geographically separated, one center being the Michigan and Ohio region while several less distinctly separated centers are scattered over the range states. Moreover there has been considerable diversity of ideas as to how much emphasis should be placed on wool, on mutton, or on this or that detail of type. This has gone to the extent of having separate classes for "B" and "C" Rambouillets at most shows where Rambouillets are important. Such classification of the individual sheep is on the basis of its own appearance with no regard to the classification of its ancestors.

Nature of This Study

The main objects of this study were to find the part played by inbreeding in the development of the Rambouillet in this country, whether the breed has developed as a homogeneous unit or has shown a tendency to split into genuinely distinct families or subgroups, and how much influence individual animals have had upon the breed.

The method used was that devised by Wright and McPhee[8] and applied by them to the Shorthorn breed.[4]

Similar studies using Wright's coefficients of inbreeding and of relationship but working largely or entirely with complete pedigrees instead of sample lines from pedigrees have been made of the Duchess family of Shorthorns bred by Thomas Bates,[6] of the Clydesdale horse[2] and of the Jersey cattle.[5] No other systematic studies of whole breeds by these methods have come to our attention.

Some 280,000 Rambouillet sheep had been registered and the pedigrees of the first 260,000 of these were available in printed volumes of the flock book when the present study was begun. For this study four samples were selected, one each from the volume containing the pedigrees of the sheep dropped in 1926, in 1916, in 1906, and in 1896. Each sample except the one for 1896 consisted of 200 rams and 200 ewes. The 1896 sample consisted of 163 rams and 219 ewes, those being all of the registered sheep born in that year. After the study was complete, another sample of 200 ewes and 200 rams was taken from among those dropped in 1926 and a similar duplicate sample was taken from those dropped in 1916, the duplicates being chosen so that no pedigree used the first time was included in the duplicate sample. The duplicate samples were used to test the accuracy of the findings from the first samples.

The method of selecting the pedigrees for each sample was to take the first animal registered on each page (or whatever other interval would result in a sample of the desired size) of the volume being sampled, with no attention to the name of the breeder or owner. Where by reason of sex or date of birth the selected pedigree could not be used, the first following one of the right sex and with the right year of birth was used. Punched cards and tabulating machines were found very useful in assembling the data from the pedigrees, more especially for bringing together the appearances of each ancestor.

The Part Played by Inbreeding

Wright's coefficient of inbreeding measures the degree of likeness (expressed in terms of correlation) between the uniting egg and sperm, relative of course to the average amount of genetic unlikeness between the gametes produced by the foundation stock. It also expresses the per cent decrease in the number of genes heterozygous in the animals whose pedigrees are being examined as compared with the number of genes heterozygous in the foundation stock. Perhaps the best way to express this in stockman's language is to say that it measures the percentage of those characteristics which were fixable but not yet fixed in the foundation stock and which the inbreeding system itself has brought into fixation. It does not include possible modification of the rate of fixation through the selection of sires and dams more homozygous than the average of their generation (as may have occurred to a slight extent) or less homozygous than the average of their generation (as very likely did occur to some extent since the breeder's striving after size, vigor, fertility, etc., would probably bias his selections a bit in favor of the more heterozygous animals).

This decrease in heterozygosity is a purely statistical consequence of the random sampling which takes place among gene pairs in Mendelian segregation. If the number of breeding individuals in the population is limited (as it is in inbreeding systems) one or the other of the allelomorphic genes in each pair may be expected eventually to become lost purely as a matter of chance and the remaining one will thus be fixed, even in cases where neither gene had a selective advantage over the other at the start. Like any other statistical process this decrease in heterozygosis has a sampling error dependent primarily upon

the variability of the population and upon the size of the sample drawn, i. e., upon the number of unfixed gene pairs at the outset and the number of individual animals for which the heterozygosity is being estimated. If the number of initially unfixed genes is very large the coefficient of inbreeding will be highly reliable even for individual animals. If the number of initially unfixed genes is very small the coefficient may be erratic when applied to individual animals but will still be reliable when applied to whole groups of animals such as a herd, a family, or an entire breed.

Besides this intrinsic sampling error which is inherent in Mendelian inheritance, there is an additional sampling error where skeleton pedigrees are used as they were in this work. This sampling error from the use of incomplete pedigrees is the basis for the probable errors[8] presented here. The other sampling error—that intrinsic in Mendelian inheritance—of course cannot be measured without first knowing how many pairs of unfixed genes there were in the average individual in the foundation stock. There seems to be no prospect of ever getting very definite information about that, although each year of genetic research brings additional indications that even in the purest strains or breeds of naturally cross-fertilized organisms, the number of such unfixed genes must be very large and far beyond that assumed by most of the early workers in Mendelism.

The percentage of inbreeding found in each sample is shown in Table I and in Figure 5. There has been a slight increase in homozygosity of the breed during the past 30 years on account of the breeding systems followed, in addition to whatever may have been accomplished by selection. The average individual animal in the breed in 1926 was about 5.5 per cent less heterozygous than the foundation animals were. The differences from period to period may be partly due to random sampling, yet they are rather what one would expect from the known history of the breed. The importations which had taken place so frequently just before the 1896 lambs were dropped and the fact that the foundation stock had been registered so shortly before would have permitted the first sample to show much inbreeding only if a large proportion of the breeders had been practicing very close inbreeding — something which apparently never happened. The inbreeding found in 1896 is about what would be expected from the average degree of relationship (to be discussed later) of all the animals in the breed to each other. In short, the breed was small and in the hands of a few breeders and there was at that time no evidence of a tendency for it to split into genuinely different families or sections.

TABLE I.—Inbreeding and *Inter Se* Relationship Coefficients

Year	*Pedigrees sampled*	*Inbreeding Coefficient*		*Relationship*
		Actually found	*Expected from inter se relationship*	*Actually found*
1896	382	2.2±.4	2.7	5.2±.8
1906	400	3.8±.4	.8	1.5±.6
1916	1200*	3.7±.3	1.4	2.7±.4†
1926	800	5.5±.4	1.4	2.6±.4

*Only 800 different pedigrees were used but one set of 400 pedigrees was sampled a second time as part of an empirical study of the accuracy of this method of tracing random ancestral lines back from sire and from dam.

†Only 800 pedigrees involved.

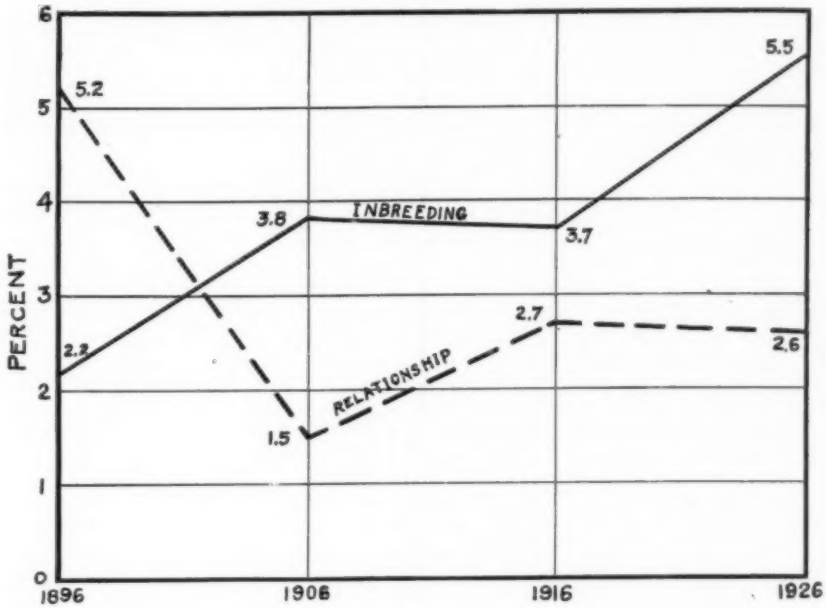


Figure 5

The Coefficients of inbreeding and of relationship from 1896 to 1926.

The prominent importations of 1899 to 1904 would have affected the 1906 sample in the same way although many of the lines in this sample could show the effect of breeding within flocks all of which had been registered for fifteen years or more. Apparently the breed had grown rapidly and some of the breeders had held aloof from the new importations while others had enthusiastically turned to them. There was already a real tendency for different families to form and for the breed as a whole to become less uniform, although the families within it were becoming more uniform.

The amount of inbreeding actually found in 1926 was nearly four times as much as would have been expected if all the inbreeding had been due to the average relationship of all animals in the breed to each other. The difference is something like seven or eight times its probable error and must therefore be judged significant. Evidently there is a distinct tendency for the breed to separate into different families although the breed probably contains no families where this has gone far enough to justify their being called inbred strains or to lead one to expect that the individuals of such families would to any marked extent, resemble each other and differ distinctly from the individuals of other families. The observed tendency for the breed to break up into separate families may be just a natural consequence of the geographical discontinuity of the breed and only in small part the result of a linebreeding policy deliberately adopted by the breeders.

Average Relationship Within the Breed

Wright's "coefficient of relationship" is the likeness (measured in

terms of correlation) to be expected between the genotypes of individuals related by descent. The coefficient of relationship may be used to measure the relationship of one individual to another, of an individual to the breed, or of a group of individuals to the breed.

The average *inter se* relationship found at the different periods is shown in Table I. In 1896 the breed was relatively small. Only 3,202 sheep had been recorded from 1889 to the end of 1894, and only 382 sheep dropped in 1896 were registered. Up to 1900, only 92 certificates of membership had been issued by the Rambouillet Association. Considering the fact that the breed was relatively new in this country, with a small number of breeders and few sheep, there would naturally have been a considerable interchange of breeding stock between breeders, all of which would tend to make the breed a unified group with all animals related to each other. That such a situation actually existed is indicated by the fact that the coefficient of relationship between individuals born in 1896 was 5.2 per cent. In comparing two random lines each traced back *from a different sheep,* one was just as apt to find a common ancestor as when comparing a random line traced back from the sire with one traced back from the dam *of the same sheep*. In other words, sires and dams were no more closely related to each other than random members of the breed were.

In 1896 the relationship of any two animals picked at random from the breed was nearly as close as that between animals having one grandparent in common and no other relationship. After 1896 there was a sharp decline in average relationship. Presumbaly the importations of the following decade were not equally distributed among the different breeders, some of whom enthusiastically sought imported sheep while others kept little but animals whose ancestors were already in the breed before 1896.

Since 1906 there has been a slight rise in the average *inter se* relationship, which is a natural consequence of the cessation of importations and of the fact that the different branches of the breed were not kept entirely isolated from each other. That there was partial isolation of this kind is evident from the fact that *inter se* relationship did not rise nearly as rapidly as the inbreeding coefficient did. In 1926 the average relationship between any two lambs was a little less than if one had been the grandson and the other the great grandson of the same ram but otherwise unrelated. This is only about half as close as the *inter se* relationship in 1896.

Relationship of Individual Animals to the Breed

The ancestors which have had a really important influence on the breed were found by counting the number of times each appeared in the random ancestral lines of each sample. A sheep found often in this random way has had a good chance to spread its genes through the breed.

The total relationship of an animal to the breed depends upon two things besides its own inbreeding coefficient: (1) the number of sons and daughters it leaves and the extent that their descendants are used in purebred flocks, and (2) its collateral relationship to the breed through other descendants of own ancestors. Thus two animals might each be found 20 times in the sample of 800 lines but the first might have several brothers, uncles and cousins which were often found in other lines while the second might have neither brothers nor sisters and might be out of parents which had neither brothers nor sisters which left any registered descendants. The two animals would have had equal influence individually on the breed but genes like those of the first would be more widely spread

through the breed because many of his brothers, uncles and other near kin would have had some of the same genes he did, and would have transmitted them to the breed.

Since not all ancestors could be investigated, attention was limited to those which appeared at least 20 times in a sample of 400 pedigrees. Those which appeared a least 20 times in at least two such samples, together with a few others which for other reasons seemed important are shown in Table II. This table therefore includes all animals which had a direct relationship to the breed as high as 2.5 per cent in two or more of the periods sampled. Doubtless there were other animals with collateral relationships to the breed higher than some of those shown but which had no very important direct influence on the breed. An important example is the ram Thomas Wyckoff 801 (10260) which in 1926 had a total relationship of 6.1 per cent to the breed but exerted his direct influence nearly all through his double grandson, E. M. Moore 26, and owed most of his collateral relationship to his half brothers and sisters through his sire, Bernardin.

The biggest changes in the importance of the various animals took place between the 1896 and 1906 samples. This is probably a consequence of the prominent importations which were made between those dates. As the later imported animals became prominent they naturally crowded many of the earlier ones back into

TABLE II—Relationship of Individual Animals to the Breed

Name	Birth Date	Registry Number	Relationship 1926	1916	1906	1896
*Hinuber	1888	328	1.8%	3.0%	1.6%	6.2%
**Von Homeyer 692	.....	922	4.8	5.4	2.0	.8
*Marie Lowe (ewe)	1889	952	4.5	4.9	1.8	.7
*Bernardin	1890	961	7.0	6.1	3.7	1.2
**Von Homeyer 560	1889	1230	2.0	1.9	1.7	8.7
**Von Homeyer 659 (ewe)	1886	1245	1.1	1.2	1.7	5.8
*(Von Homeyer)	1891	1268	2.6	2.6	3.3	14.4
*Christian 310	1892	2937	4.0	5.4	3.6	1.9
*Granson 310-8	1892	2938	.6	.4	1.1	6.1
*Hugo	1892	2940	2.4	2.5	3.1	.1
Orchard Lake	1899	13402	6.3	5.8	3.2	....[c]
Ranzin Prince	1887	13405	2.7	2.8	1.7	....
Ray R1 (ewe)	1891	13406	2.9	3.7	2.1	....
Ray R4 (ewe)	1893	13411	4.2	4.9	3.0	....
M & P 53	1895	13420	5.0	6.1	3.7	....
Kaiser (Ray R12)	1897	13435	5.4	7.2	4.7	....
Ray R14	1897	13436	4.3	7.3	3.1	....
Ray R35	1899	13442	6.4	8.0	4.7	....
Baron (A. A. Wood & Son 3)	1900	13454	5.9	6.0	3.2	....
A. A. Wood & Son 20	1901	17519	5.5	6.2	2.0	....
*Thirouin-Sorreau 446	1899	20079	3.0	1.9	1.2	....
American Boy	1902	29516	5.9	6.6	2.8	....
Baldwin 299	1903	31522	3.1	1.0[a]	.8	....
Ray's Commander	1904	37853	5.4	5.3[a]	1.9	....
*Thirouin-Sorreau 737	1904	39516	2.8	.9	....	....
E. M. Moore 26	1905	39636	7.8	5.9	....	....
Ben Hur	1906	52810	5.3	5.8	....	....
Monarch	1917	98869	7.0	2.1[b]	....	....

* Imported.
** Not imported but registered.

[a]Second sample only.

[b]Second sample only. All his relationship here to the breed is collateral of course (three-fourths of it through his descent from E. M. Moore 26).

[c]Dotted lines indicate relationship not calculated. In most cases it could not be as many of these were out of stock imported after 1896.

unimportance. This was the fate of Hinuber (328), of the von Homeyer ram (1268) and his parents (1230 and 1245) and—most conspicuous of all—of Granson (2839). On the other hand von Homeyer 692 and his son Bernardin and Marie Lowe (the dam of Orchard Lake and several other less prominent animals) were unimportant in 1896 but rose to positions of prominence in 1906 and have continued to hold that prominence even through 1926. The numerous rather important changes between 1906 and 1916 suggest that some new flocks were coming rapidly to the front as sources of seed stock and other once prominent flocks were becoming unimportant. Likewise the close agreement between 1916 and 1926 for most ancestors hints that the breed was becoming stabilized at levels of relationship which are not apt to change greatly as far as many of these long-dead ancestors are concerned. Aside from the rise of Monarch, the only noteworthy changes from 1916 to 1926 are slight decreases in the importance of Kaiser, Ray R14 and Ray R35 and some increase in the importance of Baldwin 299 and E. M. Moore 26.*

An animal deserving special mention is E. M. Moore 26 (39636) which had the highest coefficient of any animal in 1926. While this ram had a rather high direct relationship, 5.2%, its collateral relationship was largely due to the fact that "Bernardin" (961) was its only great grandsire and "Wyckoff 801" its only grandsire, and it traced to "Von Homeyer 692," eight times. This ram was therefore rather highly inbred (28.5%). This fact together with his extensive use, has resulted in his having a comparatively high relationship to the breed.

Many of the animals appearing in the upper part of Table II are ancestors of the ones in the lower half. Ben Hur (52810) whose direct relationship in 1926 was only 2.0% through his own progeny has a total relationship to the breed of 5.3%. His high collateral relationship is largely due to the fact that Baron (13454) is his only grandsire and that he traces to Christian (2937) four times and to Ranzin Prince (13405) three times. His inbreeding coefficient was 13.8%.

The only real surprise in the figures for 1926 is the rise of Monarch (98-869) to prominence. He is the only animal of recent years found in this study who has been very important for his own contribution to the breed. Monarch's direct relationship to the breed through his own progeny was 3.7% in 1926, nine years after his birth which indicates that he and his sons and grandsons have been used very extensively to make this much impression on so large a breed. Monarch was evidently the only offspring of his sire and dam who gained fame. He was found 60 times in the 1600 lines of the 1926 sample yet neither his sire nor his dam was found even once except in the lines coming through him. The breed is now so large, with so

*The probable errors attached to the coefficients of relationship in Table II would be as follows for those based on 400 pedigrees if all the relationship were direct:

Coefficient	*Probable Error*
1.0	.20
2.0	.38
3.0	.41
4.0	.47
5.0	.52
6.0	.57
7.0	.61
8.0	.65
9.0	.68

Where part of the relationship is collateral the probable errors would be slightly less than these figures. The 1916 and 1926 coefficients are based on 800 pedigrees instead of 400 and accordingly their probable errors are only about 70% as large as these. Consequently changes of less than 1.0% in the coefficient from one period to another need not be regarded as statistically significant while changes as large as 2.0% are significant except in the case of coefficients as large as 5.0% and based on only 400 pedigrees. Changes as large as 3.0% probably must be regarded as significant in all cases.

many well-established breeding centers that no future ram is likely to become as influential as Monarch in so short a time or indeed in a much longer time unless deliberate and long-continued successful linebreeding to him takes place so that there may be large numbers of animals closely related to him even long after he is dead.

After all, the most significant fact which eme ges from this study of individual relationship is that the Rambouillet breed never has been markedly influenced by any one animal. This is in marked contrast to the Shorthorn breed where the relationship of the breed to the bull Favourite, rose to over 44% some 17 years after he was born and to 50% by the time the first herd book was published. The Shorthorn breed also had a relationship to the bull Champion of England, of about 45% by 1920. Calder in his analysis of the Clydesdale breed did not calculate relationships to the whole breed but from the amounts various sires contributed to the inbreeding coefficient of the breed, it seems certain that Baron's Pride, Darnley and Prince of Wales and probably several others each had a relationship to the breed higher than was found for any individual sheep in the Rambouillet breed. Perhaps the difference is more apparent than real and arises solely from the fact that the Rambouillet pedigrees are not known as far back as those others. If we knew the individual pedigrees of the von Homeyer flock, we might find there some individual as important to the breed as Darnley and Prince of Wales were to the Clydesdales or might learn that one of the von Homeyer rams actually imported was through collateral relationship as important to the breed as Baron's Pride was to the Clydesdales. Perhaps a still better illustration is to compare these actual findings with what might have been found about the Shorthorns if Shorthorn pedigrees could have been traced back only to 1840.

Average Number of Years Per Generation

The average length of time from one generation to the next is a matter of considerable practical interest since it will enter into the breeder's plans of what he can accomplish if he undertakes deliberately to perpetuate the influence of some noted animal by some system of linebreeding. Also, it is useful in estimating what has been accomplished in the past by the breeding systems actually followed. Moreover, this information has an economic bearing in that it will permit a rough estimate of the probable replacement rate for breeding stock and the average number of offspring one may expect from animals actually retained for breeding purposes.

The data used were the birth dates of the sample animals and of the foundation animals in which the random ancestral lines terminated and a record of the number of intervening generations. The results are summarized in Table III.

With remarkable consistency in all four samples a little over four years is the average time between generations. This figure is based upon 26,235 generations totalling 111,367 years in 4764 different random lines and averaging 4.24 years per generation for the combined samples. Possibly the average age of all registered sires and dams when their young are born would be a

TABLE III.—Average Number of Generations and Years to Foundation Animals

	Generations to foundation animals	Years to the generation	Average years to foundation animals	average birth date foundation animals
1926	8.0	4.2	33.7	1892
1916	5.7	4.3	24.6	1891
1906	3.3	4.3	14.1	1892
1896	2.1	4.2	9.0	1887

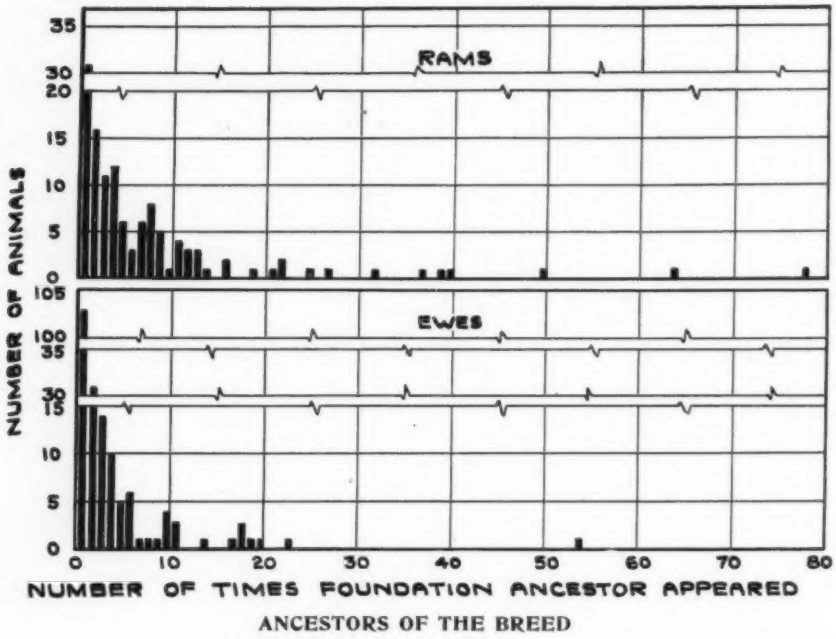


Figure 6

Number of different foundation ancestors each found at the end of 1, 2, 3 or more of the 1600 random lines traced back from the pedigrees of sheep born in 1926.

little less than this, since the method of this study eliminates data on the offspring of those animals which are used only in grade flocks and which are consequently lost to the pure breed. It is reasonable to suppose (although we do not have the data to test that) that only the most valuable breeding animals would be kept to extreme old ages and that their offspring would have a better chance of being retained in the purebred flocks than would the offspring of young and untried rams and ewes. Perhaps this makes little difference.

"Foundation" Animals

In the early days of the association, sheep were admitted to registry, (1) through certification by the owner that the sheep was imported, with its pedigree and history certified by the breeder or (2) through certification that the sheep traced "through flocks of undoubted purity of blood to importations from the royal flock of France, or the Rambouillet flock." Because of this method of registration, a line of ancestry may end in an imported animal whose sire and dam were not registered or the sire may have been registered by name and number but the dam listed only as "tracing to imported stock." Where individual records had been kept, animals were often registered along with their ancestors for as far back as the breeder had individual records. One animal was found with a birth date as far back as 1859. Because of the considerable number of animals originally registered as by some definite sire but "out of a dam tracing to imported stocks" more male than female "foundation" animals were found in this study.

Figure 6 shows the number of foundation animals which were found in the 1926 sample by this random tracing of lines 1, 2, 3, or more times each. Here 121 different foundation rams were found a total of 994 times and 192 different foundation ewes were found a total of 606 times. Yet 103 of these ewes and 31 of these rams were found only one time each while 31 more ewes and 16 more rams were found only twice each. Since these random lines necessarily had to end in some foundation animal, the finding of an ancestor once means practically nothing and the finding of it in a second line or even in a third line might be only a coincidence. However the finding of the same animal much more than five or six times by such a random method in a group of lines no larger than this, can not be ascribed entirely to coincidence. Animals found much oftener than this must occur very frequently in the complete pedigree of the breed today and the genes which they possessed must be fairly common unless real effective selection *against those genes* has been practiced among the descendants of those animals.

The 1926 sample indicates that about three fourths of the genes in the breed at that date came from the 85 foundation animals found five or more times by this method, while about half of the genes of the breed came from the little group of 31 foundation animals each found twelve or more times by this method. It may not be amiss to note that 13 of these 31 were females. We would not disparage the utility of the common slogan that "the sire is half the herd," yet it is worth remembering that about half the genes he transmits came to him from his dam and that each individual has as many female as male ancestors. The dam of more than two widely used sons may exert more influence on a breed than any one of her sons does.

Figure 7 shows the birth dates of the animals found at the end of the 4764 random lines traced in this study. No birth date was given for some of the foundation animals. In those cases we used the birth date of the son or daughter through which the animal was found. Hence the dates in Figure 7 are slightly more recent than is correct for the real foundation animals. "Von Homeyer 692," most of whose sons and daughters were born in or near 1890, alone accounts for about one third of the lines from the 1926 sample where the birth date of the real foundation animal was not known. Each individual was counted as many times as it was found and the 4764 birth dates therefore represent the birth dates of the foundation animals each weighted by the probability of its having furnished the genes of the breed at the date studied. Only a very small number of lines traced to the little group of animals found in Volume I of the Record. Many of these animals were born years before the Association was formed but their breeders and owners had kept private pedigrees and recorded these when opportunity presented.

The curves in Figure 7 show two distinct peaks separated by the almost complete absence of foundation animals born in the years 1894 to 1896. The genes prevalent in the modern breed were introduced mostly by animals born in the first four or five years after the association was formed but there was a second major introduction by imported animals born from 1898 to 1904. The absence of importations in the intervening period is not surprising in view of the severe economic depression in the wool-growing industry in the United States in 1893 and for a few years following. There are two small peaks centering on 1885 and 1881 or 1882 but the significance of their separation from the main peak is doubtful.

The average birth date of the foundation animals found in the 1926, 1916 and 1906 samples was about 1892. That for the 1896 sample was 1887, being earlier than the others because it obviously could contain none of the animals of the prominent group im-

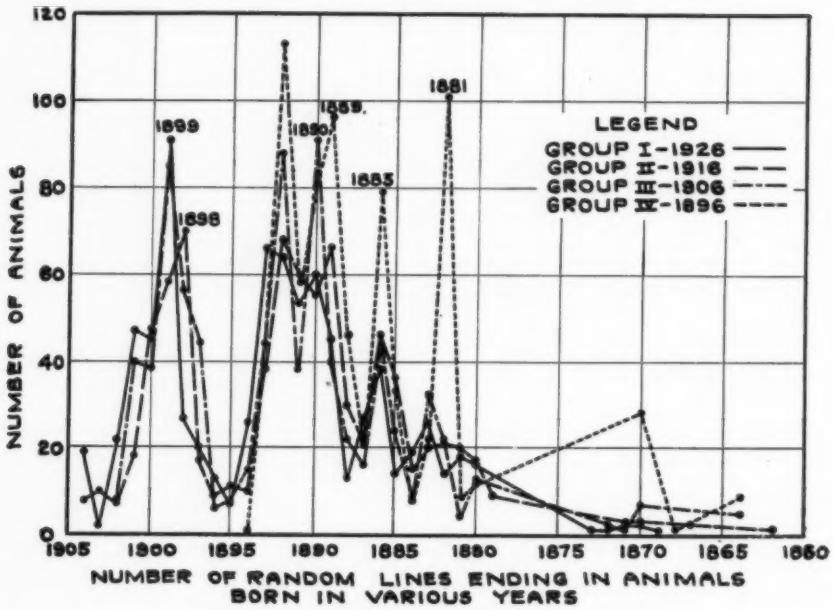


Figure 7

Birth dates of the foundation animals found at the ends of the 4764 random lines. The number of animals in the 1926 and 1916 samples (in each of which there were 1600 lines) were halved so as to show them in this graph on the same scale as the 1906 sample (800 lines) and practically the same scale as the 1896 sample (764 lines).

ported around 1898 or shortly afterward.

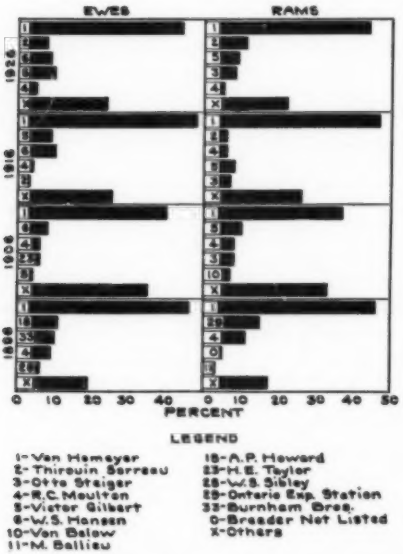
Breeders of the Foundation Animals

The breeders whose animals appeared most often among the foundation stock are indicated in Figure 8. Ewes and rams of von Homeyer breeding have in each period consistently furnished about 45% of the foundation of each group. The R. C. Moulton flock is the only other one to appear among the leading five flocks both for ewes and for rams in all four samples. However, in more recent samples it seems to have been of a little less importance than the flocks of Thirouin-Sorreau, W. S. Hansen and Victor Gilbert. The flock of Otto Steiger stands fourth or fifth as a source of foundation rams three different times but does not appear in any of the four samples as one of the five leading sources of foundation ewes.

The most impressive thing about this figure is the great influence the sheep of von Homeyer's breeding have had upon the American Rambouillet. About 45% of the genes in the breed today have come in through von Homeyer sheep unless selection for or against those genes (as distinct from selection for or against the descendants of von Homeyer sheep) has been widely and effectively practiced.

Effect of Errors in the Records

At least a few errors creep into the records of even the most carefully conducted breed registry society. Such



BREEDERS OF THE FOUNDATION ANIMALS

Figure 8

errors would affect the conclusions from a study like this in different ways according to whether they were errors resulting from carelessness or from deliberate fraud on the part of the man signing the application for registry. Errors of the former kind (including typographical errors and possible mistakes even in our careful copying and assembling of these registration numbers) would tend to make prominent ancestors appear less prominent than they really were, merely because the prominent ancestors are few and the alternatives into which they might be thrown by a clerical or typographical error are many. In the same way such errors would tend to minimize the inbreeding and *inter se* relationship coefficients.

Errors arising from false registration would tend to affect the conclusions in the opposite direction since, wherever false statements were made, the registration numbers of sires or dams as prominent and popular as possible would be substituted. The only curb on this tendency would be that the man submitting the registration application must be the owner of the named sire and dam or have written evidence of his right to register lambs from such matings. At least a little fraud of this kind creeps into every set of herdbooks but naturally there is no sound basis for estimating the amount of such contamination. Perhaps as accurate a study as can be made of that in an objective manner is the one by McPhee[3] on sex ratios and combinations in swine litters and even his study would not have detected frauds where the litter size and sexes were reported correctly but a wrong sire or dam was named.

It is some comfort to reflect that these two kinds of errors are in opposite directions although one has no right to assume that they are of equal magnitude. At any rate this study of the Rambouillet breed has shown little influence even by the most prominent sires and only a moderate amount of inbreeding. If there were very many fraudulent registrations then the true situation must be that these individual animals have had even less influence than the figures indicate and that the actual amount of inbreeding in the breed is even less than was found.

General Considerations

It will occur to some that the inbreeding and relationship found may have been only a natural result of the small number of foundation animals and the fact that the flock book was entirely closed to the registration of outside blood. Wright[7] (page 109) gives the following approximate formula for a closed population mating at random:

$$\text{Portion of existing heterozygosis lost per generation} = \frac{1}{8N_m} + \frac{1}{8N_f}$$

N_m is the effective number of breeding males and N_f is the effective number of breeding females. In domestic ani-

mals N_f is so much larger than N_m that the fraction involving N_f may be neglected without material error. An inbreeding coefficient of 5.5% in 1926 at the end of 8.0 generations is .69% per generation. That yields a value of about 18 for N_m but this is valid only on the assumption of random mating within the whole breed. The inter se relationship coefficient shows that the breed was somewhat separated into sections or families held partially aloof from each other. The *inter se* relationship of 2.6% in 1926 would have been a natural result of random mating for eight generations in a closed population where N_m was about 73. The inbreeding and the *inter se* relationship coefficients would both be satisfied with N_m about 73 but with the breed divided into at least five or six groups or families with mating nearly at random within each group but with only a little interchange of breeding stock between groups. However that picture would permit few if any individuals to rise above a relationship of 3 or 4% to the breed (less than that for the earlier imported ancestors) and does not entirely agree with breed history obtained from other sources.

The systems of breeding actually used in the Rambouillet breed seem to be about as follows:

There are far more than 73 rams in breeding use but most of these have no sons or grandsons which go to head purebred flocks. Consequently their influence on the breed is quickly diluted. Others on the contrary are highly esteemed for their own merit or are used in prominent flocks and have several sons go to head purebred flocks. Matings among their descendants bring about a certain amount of inbreeding. Here and there an occasional breeder deliberately seeks to linebreed to the choicest individuals of which he knows. The breed is loosely divided into a number of sections with only occasional interchange of breeding stock between sections but with rather free interchange of breeding stock within each section. Deliberate inbreeding that is at all intense is rarely practiced. There is at all times, more seeking after the sons of a few currently prominent sires than is implied in the term, random breeding.

Improvement of the breed would take place much more rapidly than at present if flocks above the breed average in merit were so grouped that each group would contain three to five rams of breeding age and many ewes. Animals originating in flocks outside the group would be introduced very reluctantly. Even then such introductions would usually be at least sired and perhaps also grandsired by animals bred in the group. Within each such group, breeding stock would be interchanged freely with little attention to pedigree (except to avoid too close inbreeding) but with as much attention as possible to individuality and to the merit of the progeny. Such partial isolation would soon result in each such group becoming very uniform but perhaps distinctly different from a neighboring group which might have started out with much the same kind of foundation stock. When that happens selection *as between groups* can become far more effective than at present and in particular it can be effective for characteristics which are so much affected in the individual animal by environment and by accidents of development that mass selection can make but very slow progress.

The principles of such a system are essentially those which have been used irregularly in developing the pure breeds. The idea of isolation gave us the term, "pure" breeding in the first place. The same idea has sometimes been manifested in extreme form within the limits of a single breed as when men spoke of breeding "pure" Duchess Shorthorns or argued about "pure Scotch" and "scotch-topped" Shorthorns or about "straight-bred Anxiety" Herefords. Isolating the descendants of a particularly desirable ancestor and breeding them together without intro-

ducing animals totally unrelated to that ancestor is the essential idea in the widespread practice of "linebreeding."

The important thing is that there be the right balance between the isolation (inbreeding) intensity and the effectiveness of selection. Isolation of itself works neither good effects nor bad. It merely guarantees the fixation of traits of some kind and that the groups will become uniform enough within themselves, and different enough from other groups, so that selection can become more effective than it ever can without such isolation. Isolation largely determines the *rate of fixation* but selection determines its *direction*. Too much isolation will lead to the fixation of undesired traits in spite of selection. Too little isolation means slower progress and a needless waste of time. Time is one of the most important elements in the economic application of genetic principles. The wiser and more effective the selection is, the more intensive inbreeding can be practiced with the same degree of safety.

Enough linebreeding is being done in the Rambouillet breed to bring about some progress in fixation of traits thought desirable, but progress in that direction seems needlessly slow. At the present rate it will take a hundred years to fix 15% of the fixable but now unfixed traits and it seems reasonably certain that twenty-five years ought to be time enough to accomplish that without running any real risk of fixing undesired traits in the whole breed.

Summary

The inbreeding coefficient for the American Rambouillet breed of sheep rose to 5.5% in the 34 years (8 generations) ending in 1926.

The coefficient of relationship between random animals born in 1926 was 2.6%.

No one ancestor has ever had a very dominant influence on the breed. The maximum relationship found between one animal and the breed was 14.4% for a von Homeyer ram (1268) in 1896 when the breed was newly organized and small. No other animal has exceeded 8.7% and few have exceeded 6.0%.

The average interval from generation to generation is 4.2 years.

Most of the ancestral lines end in animals born in the few years immediately preceding 1894 but many imported ancestors were born from 1898 to 1904 and a few ancestral lines are known even further back than 1880.

About 45% of the ancestral lines end in animals bred by von Homeyer in Germany. No other firm bred more than 10% of the foundation animals.

Breeding systems which might lead to more rapid improvement in the breed are discussed.

Literature Cited

1. Bernardin, L. 1890. La Bergerie de Rambouillet et les Merinos. (English translation—Summary of this is in Volume 1 of American Rambouillet Record.)

2. Calder, A. 1927. The role of inbreeding in the development of the Clydesdale breed of horses. *Proc. Royal Soc.*, Edinburgh, Val. 47, Part 2, No. 8:118-140.

3. McPhee, Hugh C. 1927. The swine herdbook as a source of data for the investigation of the sex ratio and frequency of sex combinations in pig litters. *Jour. Agr. Research*, 34:715-726.

4. McPhee, H. C. and Wright, S. 1925, 1926. Mendelian analysis of the pure breeds of livestock. III. The Shorthorns, *Jour. of Heredity* 16:205-215. IV. British Dairy Shorthorns. *Jour. of Heredity* 17:397-401.

5. Smith, A. D. B. 1926. Inbreeding in cattle and horses. *Eugen. Rev.* 14:189-204.

6. Wright, S. 1923. Mendelian analysis of the pure breeds of livestock. II. The Duchess family of shorthorns as bred by Thomas Bates. *Jour. of Heredity* 14:405-422.

7. Wright, Sewall. 1931. Evolution in Mendelian Populations *Genetics* 16:97-159. See especially pages 107-111.

8. Wright S. and McPhee, H. C. 1925. An approximate method of calculating coefficients of inbreeding and relationship from livestock pedigrees. *Jour. Agric. Research* 31:377-383.

Books Received

BOOKS are acknowledged in this column as received, and such acknowledgment must be regarded as sufficient return for the courtesy of the sender. As far as space permits, books that contain material of special interest to the reader of the JOURNAL *will be reviewed in later numbers.*

OUR CHILDREN, A HANDBOOK FOR PARENTS. *Editors,* DOROTHY CANFIELD FISHER and SIDONIE MATSNER GRUENBERG. Prepared and sponsored by the Child Study Association of America. 29 Chapters by 29 Authorities. Pp. 348. Price, $2.75. New York, The Viking Press. 1932.

In the sense that we *know* about matter and gravity and the flow of fluids through pipes and the mechanical equivalent of heat, we *know relatively nothing* about the care and rearing, especially the psychic and psychological rearing of human young. This book summarizes our lack of knowledge very completely and in a way that is not painful. In fact we might almost believe our ignorance to be wisdom, if not bliss.

THE CHANGING CULTURE OF AN INDIAN TRIBE. *By* MARGARET MEAD, Assistant Curator of Ethnology, American Museum of Natural History. 3 Parts; 16 Chapters. Pp. 313. Price, $4.50. New York, Columbia University Press. 1932.

One view of what the Paleface does to the Redskin in these later days.

CONTEMPORARY SOCIAL PROBLEMS. *By* HAROLD A. PHELPS, Ph.D., Professor of Sociology, University of Pittsburgh. 4 Parts; 21 Chapters. Pp. 783. Price, $3.50. New York, Prentice-Hall, Inc. 1932.

These arise chiefly for two reasons: (1) disregard and disdain of the factor of heredity in human affairs; (2) the above-mentioned almost complete ignorance as to what is a good environment for the young of the genus *Homo.*

GRUNDLAGEN, WEGE UND ZIELE DER OKOLOGISCHEN HAUSTIERGEOGRAPHIE. *By* STEFAN TAUSSIG. With 11 illustrations and 3 colored plates. 121 pages. Verlagbuchhandlung Paul Parey, Berlin, 1932.

PARENTS AND SEX EDUCATION, For Parents of Young Children. *By* B. C. GRUENBERG. 7 Chapters. Pp. 112. Price, $1.00. New York, The Viking Press. 1932.

Perhaps the "sex uproar" which so disturbs and delights Henry Louis Mencken will be wiped out by Dr. Gruenberg's making it all sound a matter of course. Unfortunately (perhaps providentially) the respective male and female sex hormones, even discovered and isolated, do queer things to the organism-as-a-whole.

FLORIDA WILD LIFE, *by* CHARLES TORREY SIMPSON. Pp. XII + 199, many illustrations. Price $2.50. New Vork Mcmillan Co., 1932.

From the fund of his vast knowledge of the living forms which make Florida fascinating, Dr. Simpson gives us a glimpse of this only tropical part of the United States, which he has studied so fruitfully for so many years. With the Everglades National Park to the fore this book is especially timely.

THE SORCERERS OF DOBU, *by* R. M. FORTUNE, M. A., Ph. D., with an introduction by B. MALINOWSKI. Pp. XXIV + 318. Many illustrations. Price $5.00. E. P. Dutton Co., 1932.

The social anthropology of the Melanisian Dobu Islanders emphasizes again that the superficially simple life of the scarce-clothed savage is an extremely complicated affair. It has even been suggested with some plausibility that the savage remains a savage because he has so many social "shalts" and "shalt nots" to attend to that the time available after these are out of the way suffices only to make possible a bare existence.

REXING THE LILAC RABBIT

Inheritance of Four Coat and Color Factors Demonstrated in the Domestic Rabbit

RAYMOND T. PARKHURST and W. KING WILSON
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THE manner in which unit-characters disappear and reappear due to the combination, segregation, and recombination of genes is well illustrated by the results obtained from experiments in the Department of Rabbit Husbandry of the National Institute of Poultry Husbandry, Newport, Shropshire, England.

The object of the experiment was to demonstrate the transmission of the "rex" character from a relatively new variety of rabbits to a well established utility breed. The Lilac normal-coated rabbit and the Castorrex were chosen for the experiment as, in addition to the rex factor, at least three known unit-characters for color would be involved.

During the summer of 1929, a typical Castorrex buck was mated to 14 typical Lilac does and 38 F_1 individuals were obtained, which were all wild grey (agouti) in coat pattern and coloring. The mating *inter se* of selected F_1 bucks and F_1 does began in February, 1930 and by September, 1931, records had been obtained of 524 F_2 offspring from 9 bucks mated to 19 does.

Four Unit-Characters Involved

The "rex" character (the formula for which is *r*) is recessive to normal coat and according to Castle[1] shows no linkage with any other mutant gene. Rabbits that are homozygous for this character (*rr*) have a mole-like coat consisting of short hairs of fine texture. The normal rabbit fur contains "guard" hairs that are relatively long and coarse and which are in many cases plucked from the skins before they are made into fur garments.

The "wild" or ordinary gray coat character is due to the presence of the dominant factor for Agouti (*A*). The alternative recessive concerned in this study is self (*a*). The agouti factor (*A*), when present in the zygote, turns the black character to agouti, blue to blue agouti, chocolate to chocolate agouti and lilac to lilac agouti. "Selfs" (genetically *aa*) have no band of yellow on the ordinary hairs of the coat or white tip to the hairs on the undersurfaces; i. e., the belly and the underside of the tail.

Agouti rabbits, including the Castorrex, have a dominant factor (*B*) which causes the development of black and its alternative recessive is (*b*) which brings about a change from black pigment to brown (chocolate). In addition, there is a factor (*D*) present in the Agouti which in its recessive form is responsible for bringing about the dilution of color. Blue is produced by diluting black, and lilac is the result of diluting chocolate. Expressed in another way, (*D*) is the factor which turns lilac into chocolate and *B* is the factor that turns it into blue. Lilac is a triple recessive for color containing the recessive factors for agouti, black, and dense pigment. Thus all lilac individuals have the formula *aa bb dd*. The addition of the black factor (*B*) to lilac produces blue instead of black because of the presence of the dilution factor (*d*). When *B* (black) and *D* (dense pigment) factors are together, they give black in the absence of factor (*A*) for agouti.

The Castorrex rabbit has a genetic constitution of *rr AA BB DD;* i. e., it contains double doses of the recessive factor for rex, and dominant factors

A CASTORREX BUCK

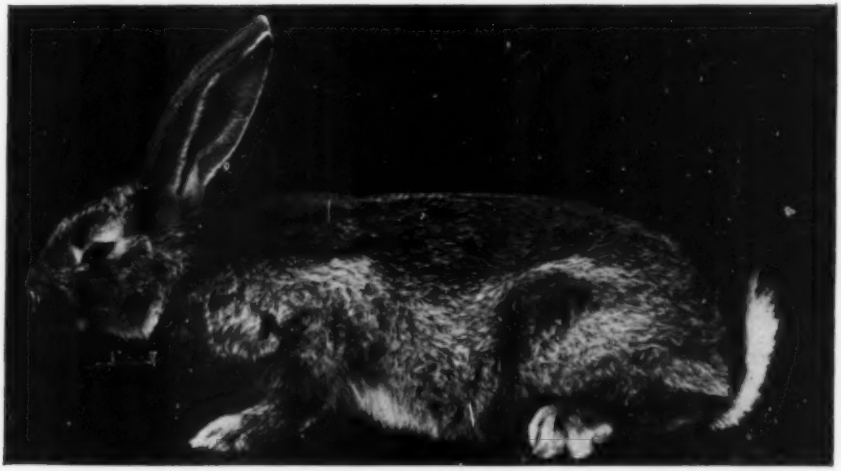
Figure 9

The castorrex rabbit is pure (homozygous) for three dominant genes affecting color: *A*, the gene determining the wild type coat; *B*, the gene determining black (in the absence of *A*), and *D*, a "dilution factor" (the recessive allelomorph of which changes black coat color to chocolate). In addition this breed is also pure for the recessive "rex" which produces the plush-like coat due to the atrophied or absent guard hairs. The rex gene also affects the whiskers which are small and deformed.

LILAC NORMAL (NON-REX) DOE

Figure 10

The normal-coat lilac may be said to be a castorrex turned genetically inside out. It is homozygous for the recessive allelomorphs (*a. b. d.*) of the color genes for which the castorrex carries the dominants, and it has the normal long-hair allelomorph of the rex gene. Thus the genetic color and coat formula of the pure castorrex is *AA BB DD rr* and that of the pure normal lilac is *aa bb dd RR*. It is obvious that the offspring of such mating will carry both members of all four pairs of genes and its constitution will be *Aa Bb Dd Rr*. One can predict that all of the offspring of such a mating will be normal wild-type agouti in appearance. Such a rabbit is shown in Figure 11.



THE FIRST GENERATION HYBRID

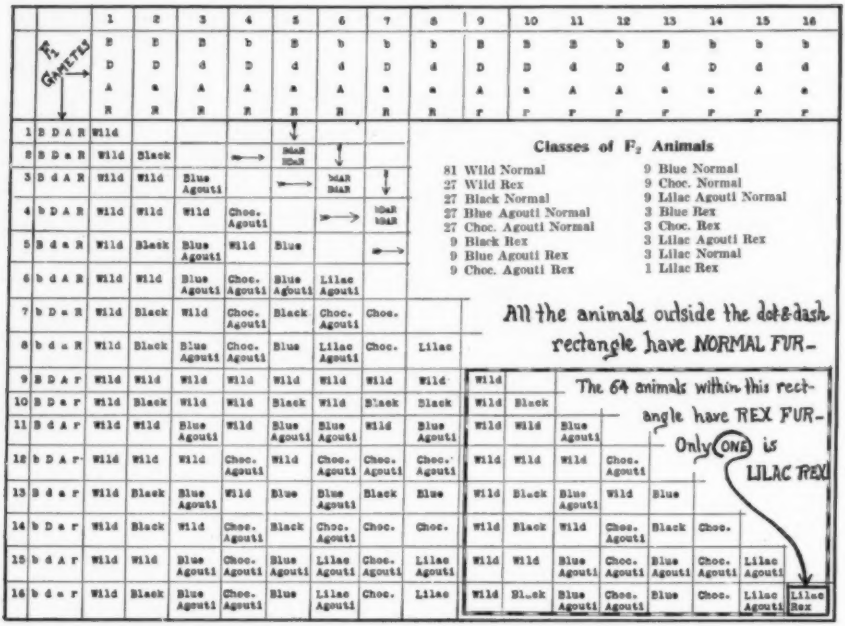
Figure 11

Rabbit produced by crossing castorrex and normal lilac. In appearance this is a normal wild-type rabbit, but whereas the offspring of ordinary wild rabbits are, with few exceptions, like their parents, the offspring of two such rabbits as this will vary tremendously. In order to produce all types at least 500 progeny would probably be necessary. There would be sixteen visibly different types, some 81 times as frequently encountered as others, and 128 genetic types, often looking alike but differing in the kind and proportion of their progeny.

A LILAC REX

Figure 12

Among the progeny produced by intercrossing the castorrex-lilac hybrid, the most frequently encountered form is the wild-type. A quarter of the offspring will be rex, and of these rex individuals, one sixty-fourth (of the entire progeny, less than four in a thousand) will be lilac rex. Fortunately for the practical breeder the lilac rex individuals, being pure for four recessive characters (*aa bb dd rr*), will be true-breeding. The type will be fixed, with regard to these characters, without further selection.


F1 GAMETES
Classes of F2 Animals
81 Wild Normal
27 Wild Rex
27 Black Normal
27 Blue Agouti Normal
27 Choc. Agouti Normal
9 Black Rex
9 Blue Agouti Rex
9 Choc. Agouti Rex
9 Blue Normal
9 Choc. Normal
9 Lilac Agouti Normal
3 Blue Rex
3 Choc. Rex
3 Lilac Agouti Rex
3 Lilac Normal
1 Lilac Rex
All the animals outside the dot-&-dash rectangle have NORMAL FUR-
The 64 animals within this rectangle have REX FUR-
Only ONE is LILAC REX!

EXPECTATION IN THE SECOND HYBRID GENERATION

Figure 13

"Checkerboard" showing the sixteen types of progeny and their proportions in the second generation of a cross between Lilac and Castorrex rabbits. The average frequency of appearance of the 16 types in the second generation is shown in the chart. ("Classes of F_2 Animals.) In actual breeding operations, of 524 animals 2 were lilac rex. Such animals, being pure recessives for all genes involved will breed true when mated *inter-se*.

for black, dense pigment, and agouti. The genetic make-up of the Lilac normal-coated rabbit is shown by the formula *RR aa bb dd;* i. e., it is homozygous for normal fur, non-agouti, chocolate, and dilution of pigment. The first generation (F^1) are all agouti color, have the "wild" pattern and genetically are *Rr Aa Bb Dd;* i. e., they are heterozygous for all four factors.

Figure 13 shows the distribution of gametes in the second (F_2) generation and also the classes of F_2 animals according to the theoretical Mendelian expectation.

Table I shows the number of animals of each of the eight colors expected and actually obtained, the number of each that were expected to be normal-coated and rex-coated, and the results of the experiment.

The number of rexes, and also the number of black normal rabbits obtained, were significantly less than expected. The differences in the chocolate agouti and lilac agouti classes may be partly due to mistakes in identification because of their similarity. A number of animals included in the rexes had a condition of partial furlessness, which may be partially lethal and is probably, like most other forms of furlessness, recessive. As the abnormally low ratio of rex to normal is in agreement with other workers and general observation of practical breeders the most probable explanation is a higher prenatal death rate of rex rabbits. The authors are unable, at present, to give any explanation for the sig-

nificantly low rate of actual to expected numbers in the black normal animals.

The authors gladly acknowledge the assistance of Professor R. C. Punnett, Mr. Michael S. Pease, and Mr. F. J. Dudley.

Literature Cited

1. CASTLE, W. E. 1930. "Genetics of Domestic Rabbits."

2. ———. 1929. *Jour. of Hered.*, Vol. 20, No. 5.

3. PICKARD, JAMES N., and CREW, F. A. E. 1929. "The Scientific Aspects of Rabbit Breeding."

4. NACHTSHEIM, HANS, 1929. *Zeitschrift für induktive Abstammungs-und Vererburgslehre.* 52.

5. PUNNET, R. C. 1912. *Jour. Gen.*, Vol. II, 221-38.

6. ———. 1915, *Jour. Gen.*, Vol. V, 37-50.

TABLE I.—Results secured in F_2 generation of inter se matings of Casterrex × Lilac normal F_1's.

Colour Groups	Normals Expected	Normals Actual	Approx. Differences	Rexes Actual	Rexes Expected	Approx. Differences	Totals Expected	Totals Actual	Approx. Differences
Agouti	165.79	190	+24	55.27	44	−11	221.06	234	+13
Blue Agouti	55.27	62	+ 7	18.42	16	− 2	73.69	78	+ 4
Black	55.27	42	−13	18.42	16	− 2	73.69	58	−16
Blue	18.42	15	− 3	6.14	5	− 1	24.56	20	− 5
Chocolate Agouti	55.27	52	− 3	18.42	11	− 7	73.69	63	−11
Lilac Agouti	18.42	31	+12	6.14	7	+ 1	24.56	38	+14
Chocolate	18.42	21	+ 2	6.14	3	− 3	24.56	24	−
Lilac	6.14	7	+ 1	2.05	2	−	8.19	9	+ 1
Totals	393.00	420	+27	131.00	104	−27	524.00	524	−

A Genetic Picture-Book,—and More

THE MECHANISM OF CREATIVE EVOLUTION. *By* C. C. HURST. XXI + 365 pp., 198 figs. Price $6.00. Cambridge Univ. Press (England). The Macmillan Co., N Y. 1932.

HURST has produced what may justly be called the perfect picture-book of genetics, a volume beautifully printed at Cambridge, England.

The impression, however, should not be created that this is *merely* a picture book. It contains a lucid and interesting account of the development of genetics and its relation to the theory of evolution. The author lays special stress upon the field of cytogenetics in which he has himself worked in recent years. His earlier work as an experimental breeder of animals and plants in close association with Bateson was summarized and in large part republished in a single volume, *Experiments in Genetics,* 1925.

In the present volume he lays stress upon the chromosomes and their contained genes as the mechanism of heredity and evolution. But the distinctive feature of this volume is its abundance of carefully selected figures, numbering 198, collected for the most part from the publications of a great number of other investigators and reproduced with perfect fidelity. Often the arrangement or description of the figures creates a much more telling effect than the original publication itself. Throughout the book the story is told by the pictures. But if one desired to know in a particular case whence the picture came, he might find it difficult. For the legends do not state from *what* publication of an author a particular figure was taken, and frequently credit is given to the compiler of a text-book rather than to the investigator who did the original work.

Hurst is also careless in the matter of bibliographic references, which also leads him occasionally to give credit where it does not belong or to withhold credit where it is due.

Most of the cases which he reviews as illustrative of the dependence of

heredity upon genes and chromosomes relate very properly to work on Drosophila or on plants. But his discussion of the genetics of rabbits, a field in which he himself did pioneer work, shows a lack of familiarity with what has been done in the last twenty years, since his own withdrawal from this field.

On the whole, this book will be interesting and inspiring, even to the geneticist who is very familiar with the field. It will make him realize how much good work has been done in the last thirty years in the field of genetics in relation to evolution, and he will be made to appreciate many of the fine points which he had previously failed to realize, in classic experiments. This lucidity is due in large part to the excellence of the figures and the care taken in the legends to tell enough but not too much. Hurst in this has attained the objective always kept in view by David Fairchild and the successive managing editors of the JOURNAL OF HEREDITY to make scientific exposition clearly and quickly by means of abundant and accurate figures and a sparing use of words.

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Harvard University.

Rural Sociology in a Humane Civilization

. . . . From my own observation, I found before the war that the introduction of folk-lore and local government into Elementary and Secondary schools (into the framework of which rural sociology was to be worked) left much to be desired. A responsible ministerial official assured me that at the end of the third decade of this century things are no better. The text-books and manuals of folk-lore and local government are in the view of the teacher too far removed from reality and life.

Also in the continuation schools this question must be taken more in earnest. More necessary than the introduction of the urban social and economic system in the rural continuation schools is that of the sociological problems of the rural areas in the urban continuation and technical schools, with the special proviso that this is a life and death question for the German race. To every town dweller it must be quite clear always and everywhere and remain so, that he, the townsman, not only lives by the bread but also by the blood of the countryside: that the town not only draws the best brains and muscles from the rural areas, but that the rural areas bear the cost of training them, while the town harvests the fruits of this training and cultivation.

Then through rural sociology, as half of special sociology, general social science would find a healthy basis on which questions of sociological subjects and sociological methods should be rapidly answered; then through rural sociology real 'folk-communion' could be investigated and helped. Rural sociology would be a bridge between political science and culture philosophy.

In the exact sciences the press gives great assistance by quick publication and popularizing of research and progress. In a cultural crisis this may lead to the spiritual sciences simply following with a limp; technique makes the running for life and economics. The cultural sciences and politics can only to some extent act as brakes on the wheels of developments often unfortunate. They have to limit themselves to healing the damage caused. Not this, however, but prevention, must be made the aim and object of the cultural sciences, must be the deciding factor in their policy. So long as politics remains the 'Art of the Possible' the damage to society and administration must become more and more severe, the healthy reaction be more and more checked. If, however, sociology becomes the forum of the cultural sciences, as Tönnies when President of the Seventh German Sociological Meeting advised, then politics can become the 'Art of the Necessary.' Intellect will again lead before money, humanity will keep its right to exist and its dignity as such, in spite of the machine; and the destruction of communities and the separation of groups and members of society will be checked. This will not be possible without the full collaboration of the press.

In the same way that politics and the press are the last leaders and educators of the spirit of humanity and of public opinion, so pedagogy and the parental roof are the first educators and therefore the most influential leaders of society.—RICHARD KAYSENBRECHT, Rural Sociology: A Challenge of the Times. *Sociological Review*, July, 1931. Pp. 118-119.

HERITABLE CHARACTERS OF MAIZE

XLIV—Silky Ears*

ALLAN C. FRASER†

IN the course of the genetical studies of maize at Cornell University, a number of ears have appeared which bore silks in great profusion. The condition of these ears was particularly noticeable since the silks did not break away at the time of husking, as silks usually do, but remained rather firmly attached. The writer has taken over a number of these silkies as they appeared and undertaken a genetical study of them.

No fewer than 14 silky ears have been found, and the origin of many of these in unrelated stocks has suggested that some, at least, might be genetically different. Tests of the genetical nature of the various silkies have not been completed nor have all the different tests for genetical identity been made. It has seemed best, however, briefly to describe the character at this time and to present data on two of the strains.

Silky I (si_1)

The first type to be found was called silky-I.‡ This appeared first in the genetic material of Professor R. A. Emerson. The ear of silky-I looks normal as far as cob and seeds are concerned and the rows of seed are in good alignment. Silks appear in great numbers both from between the rows and between the kernels in the row. (Figure 14.) An examination of the mature ears and of those which had not yet reached the milk stage, showed that the extra silks were coming chiefly, and perhaps wholly, from the second flower of the spikelet. This second flower in maize usually aborts. In many cases the silk from the second flower was found to be branched near its base and in others, several silks were found to be coming from the lower floret. The tassel of silky-I has an almost normal appearance, but there is a tendency for the branches to be less plump than in the normal sibs. Usually only a small number of flowers shed any pollen, chiefly those toward the upper part of the main axis of the spike. The small quantity of pollen is shed quickly, and frequently by the time the tassel is noted as shedding pollen, it is too late to bag it for any. Often a small number of thin, wiry silks will develop from the tassel, but these have never resulted in the development of seed. Silky-I differs from the true "tassel-seeds" in this respect as well as in its tendency to develop a good ear in the normal position. Axillary ears, as a rule, are only obtained in the tassel-seed types when the ovule-bearing tassels are removed. The general effect of the silky gene, or genes, both with this and the other types of silkies studied, is to make the plant almost entirely pistillate, at least with respect to function.

Numerous crosses of silky-I and non-silkies, chiefly linkage testers, gave non-silkies in F_1. The combined data on 17 F^2 families are given below.

	Normal	*Silky*	*Total*	*D*	*D/P.E.*
Obs.	1935	581	2516	48±14.65	3.28
Calc.	1887	629	2516		

While the deviations of these results from the theoretical expectancies are rather high, it is evidently due to a

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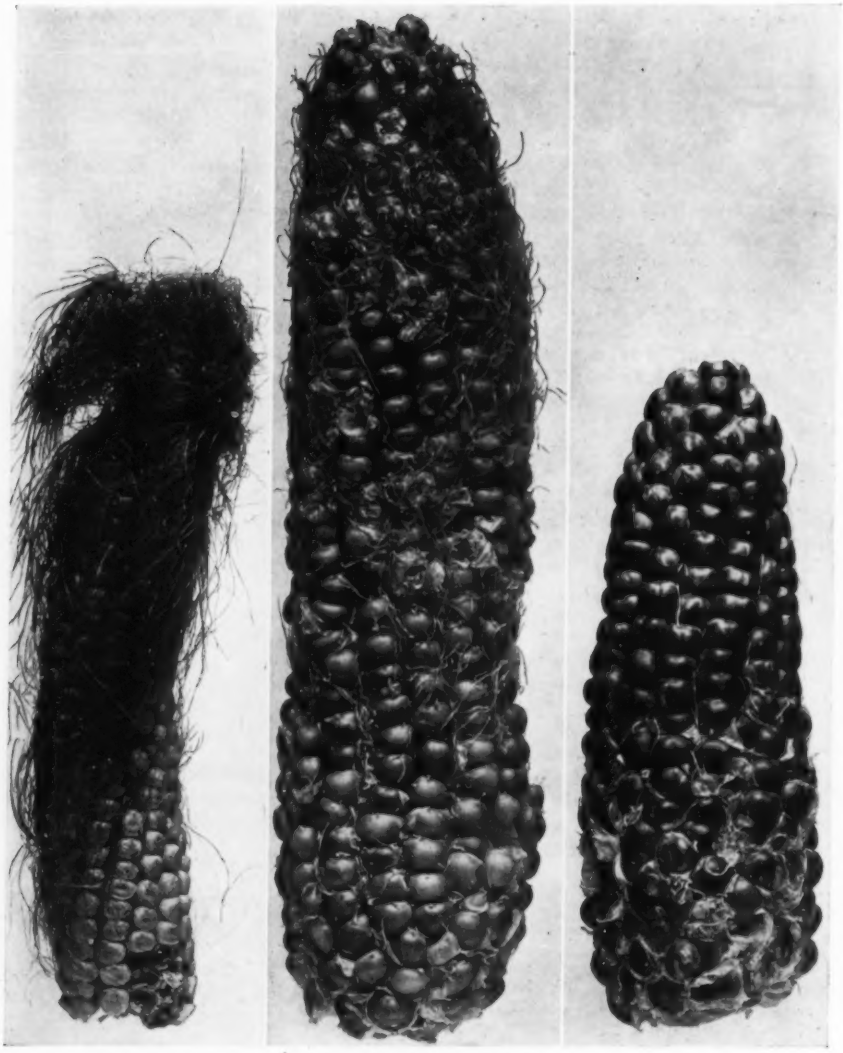
‡For convenience the silky stocks have been given acquisition numbers in Roman numerals to distinguish those of different origin. These numerals give no information as to the number of genes involved.



TWO FORMS OF SILKY

Figure 14

At the left is a single ear of silky-1. At the right are two ears of silky-II,—the "clumpy" type of silky. The ear at the right shows a less extreme development of the character than does the one at the left. These two silkies are genetically distinct.

slightly poorer viability of the silky type. Eleven of the seventeen F_2 families showed deficiencies of the silky class. In only one of these, however, was the difference between observed and calculated results greater than three times its probable error. It seems reasonable to assume, therefore, that the silky type differs from non-silky by a simple recessive gene, si_1.

Crosses of silky-I with a number of the linkage testers showed that si_1 belongs to the *Y-Pl* linkage group.

F_2 of cross *Y si* × *y Si*. (4 families)

	Y Si	*Y si*	*y Si*	*y si*	Total
Obs.	463	222	205	4	894

F_2 of cross *Pl Si* × *pl si*. (1 family)

	Pl Si	*Pl si*	*pl Si*	*pl si*	Total
Obs.	155	16	33	29	233

The calculation of strengths of linkage by use of Immer's tables shows the following percentages of crossing over:

Approximately
Y-Si — 14±2.2%
Pl-Si — 24±2.2%

While the values thus obtained are not as dependable as one might wish, when considered with their probable errors, they at least indicate that si_1 is between *Y* and *Pl* and probably a little nearer to *Y* than to *Pl*. Emerson's data show about 27 per cent of crossing over between *Y* and *Pl*. The actual map distance is presumably greater than this, but probably not as great as the sum of the two values given above. Three-point tests are now being made to determine more accurately the position of si_1. Other data now on hand show that si_1 is independent of *A, C, R, Pr, B, Lg,* and *Sh*.

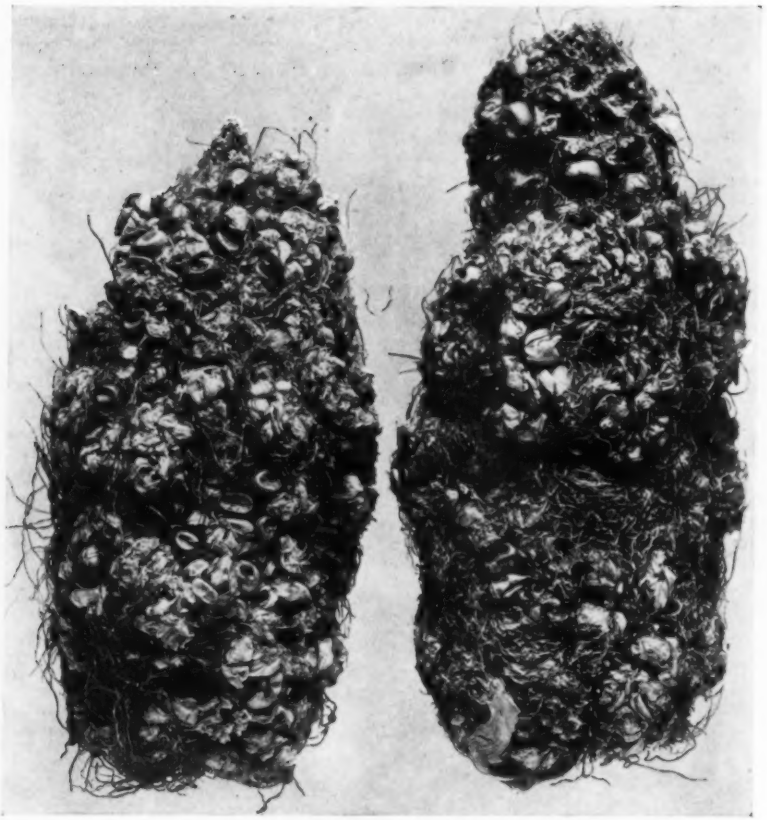
Two other silkies have been found upon crossing to be identical with, or at least allelomorphic to, *si*-I. These are *si*-IV, which appeared in one of Professor R. G. Wiggans' inbred varieties, and *si*-V, from Professor Emerson's genetic material.

Strains of silkies II, III, and X were found not to be allelomorphic to *si*-I. The intercrosses of silkies have usually been made with heterozygous material, at least in the male parent, in order to obtain an abundance of pollen for the cross.

Silkies II and III

These two silkies were found to be genetically identical as well as phenotypically indistinguishable. In its weakest expression, this type shows at several places on the ear, masses of glume-like material usually matted together and producing many silks. These masses may be wedged between the kernels, or spaced where a normal kernel would ordinarily have come. In some cases only one or two of these "clumps" will appear on an ear, and such are almost invariably near the base of the ear. In more extreme cases these clumps of silk and tissue are produced rather evenly over the ear from the butt to the tip.)Figure 14.) Occasionally this type produces a very abnormal ear which is not only very silky but also shows an unusual growth of tissue over the whole ear. When this "bungle ear" is dried, the superfluous growths can be broken off to reveal many normal seeds. These last have presumably resulted from the fertilization of the upper flower of the spikelet, and as nearly as can be determined without a detailed histological study, the great mass of over-lying tissue comes from many secondary florets which have proliferated greatly. In this tissue glume-like structures can be identified. (Figure 15.) The relation of this "bungle" type to the "clump" type of Figure 14, has not yet been determined. The fact that each of these types can "throw" the other, however, suggests that the extreme form is produced more in response to environmental influences than to genic modifiers. The relative infrequency of occurrence of the "bungle" type and the irregularity with which it appears, makes an enumeration of counts, even on large families, of little value.

The tassels of *si*-II and *si*-III are much like those in *si*I in appearance but they



A "BUNGLE" EAR

Figure 15

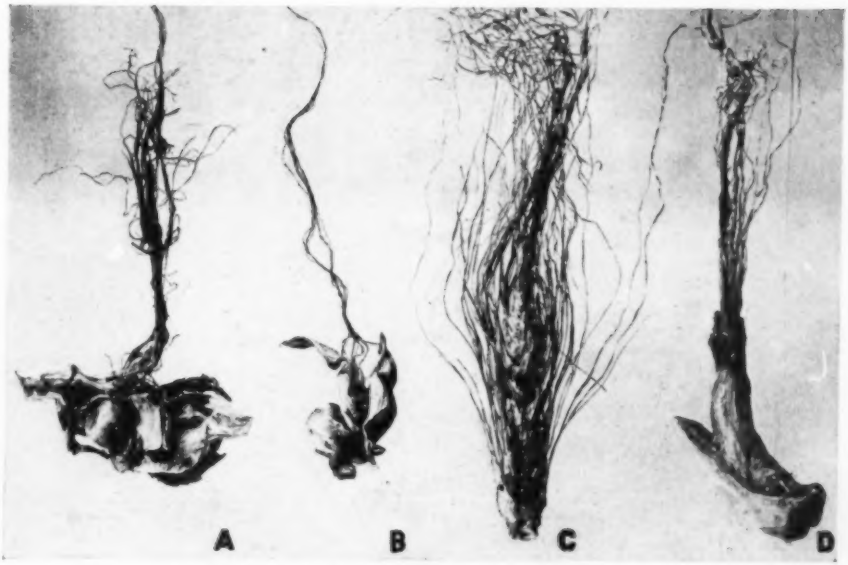
The "bungle" ear which is found occasionally in families of silky-II and III. Most of the silks have been removed to show the growth of glumes and other tissue from what appears to be the second floret of the spikelet.

tend to produce considerably more pollen than does *si*-I.

Crosses of silky-II with non-silky gave non-silky ears on most of the F_1 plants. Rarely there appeared a single clump of silks on these heterozygous ears, but no strong development of them as in the type. The F_2 gave 270 normals to 23 silkies, a close approach to the 15:1 relationship. In F_3 and F_4, both 15:1 and 3:1 segregations were obtained from this material. Evidently duplicate genes were functioning in the F_2.

Crosses of silky-III with non-silky gave behavior similar to that of silky-II. In the F_2 there appeared 189 normals to 21 silkies in one family, and 116 normals to 35 silkies in another. The first segregation looks to be on the basis of 15:1 and the second, 3:1.

Intercrosses of plants heterozygous for *si*-II and others heterozygous for *si*-III gave in two similar F_2's—126 normals :8 silkies, and in another family—53 normals : 9 silkies. The first segregation closely approaches the 15:1 relationship and the second approximates



STRUCTURE OF SILKY-TUNICATE SPIKELETS

Figure 16

(*A*) and (*B*)—mature spikelets from an ear of the constitution Si_1 si_1 *Tu tu*. At the left in each (*a*) and (*b*) is the seed formed in the upper flower, and at the right is the mass of silks coming from between the long glumes which enclose the lower flower. (*C*) shows the little ear-like structure which develops from the lower flowers, more particularly toward the base of the ear. At (*D*) is srown one of the "pods" from the base of the ear, enclosing the parts which have developed from the second flower of a spikelet.

the 7:1 to be expected in a cross where one parent is heterozygous for both pairs of duplicate genes and the second parent is pure recessive for one of these same genes and heterozygous for the other, as Si_2 si_2 Si_3 si_3 × si_2 si_2 Si_3 si_3.

No linkages have been found between either of these two genes and any of the linkage testers as yet tried.

General Discussion

A study of the F_2 silky-tunicate (si_1 *Tu*) segregates of a cross between silky-I and tunicate, offers a suggestion as to the possible origin of the extra silks in these silkies. In this recombination type (si_1 *Tu*) the first flower of the spikelet develops a seed enclosed in a pod, as is usual in the tunicate type. Just below this and bracketed by glumes is the second flower. The long glumes of this flower enclose a structure which resembles a head of two-rowed barley. (Figure 16.) It has a central rachis with what look to be small pods set along it. As this material was not examined until it had dried, the small size of the dried pods made it difficult to identify flower parts within them. It seems highly probable, however, that these tiny pods are spikelets on a small ear which comes from the second flower of the main spikelet. As each of these little pods on the diminutive spike produces a silk, there is a large bundle of silks pushing out from the glumes of the second flower. In many cases the little "secondary ears" are found almost to the top of the cob. This condition in the silky-tunicate ear suggests that the silky type

may perhaps be due to some influence which causes the second flower of the spikelet to start developing an ear-like structure, each flower of which produces a silk and gives to the main ear its very silky appearance. The degree of silkiness would then depend upon the extent to which a complete ear-like structure had been developed in this second floret. In silky-I, the development of the "secondary ear" cannot have proceeded very far, since only a few silks come from each of these lower flowers. In silky-II, however, much more tissue develops and in the "bungle" type a great mass of tissue seems to issue forth from each of the secondary flowers but with no discernible tendency to form a definite structure. It is quite possible, to be sure, that the little ear-like structures which develop in the second flowers of the silky-tunicates represent more truly a modification of the tunicate type than the silky.

The silky character is not to be recommended for linkage studies nor for genetical investigations of chromosome behavior. With a number of stocks it is practically necessary to use it in the heterozygous condition. In several of the F_1's studied and apparently in some F_2's, the silky character tended not to be perfectly recessive. The expression of the character is also affected to some extent by environmental conditions.

To Them That Hath Not Shall Be Given

SPECIAL EDUCATION: The handicapped and the gifted. White House Conference on Child Health and Protection. Report of the committee on special classes; Charles Scott Berry, chairman. Pp. 604. Price, $4.00. New York, the Century Co. 1932.

THE interest of educators in the handicapped and the gifted, respectively, is shown neatly in the division of this book. The gifted receive exactly 13 pages; the handicapped all the rest. Yet "the cost of special classes for gifted children is not necessarily greater than for the regular classes" (p. 545), while for thehandicapped (p. 11) "the annual per capita cost of education in special classes or schools is from one and one-half to four times as great as the per capita cost of education in the regular elementary schools,' 'with the one exception of speech defects.

Among the handicapped are 14,400 blind children under 20 years of age, 50,000 partially-seeing children who should be in sight-saving classes, 3,000,000 children with hearing impaired in various degrees, 1,000,000 so defective in speech tha tthey require special training, 300,000 crippled children of whom one-third need special education, 382,000 auberculous children with an additional 850,000 who are "suspicious cases," 1,000,000 school children with weak or damaged hearts, 6,000,000 malnourished, 675,000 who present behavior problems, 450,000 mentally retarded to the extent that they need special education.

It is not a cheerful picture, and even in a volume dedicated to treatment, one might have expected to find a word as to the need of prevention, also.

Valuable as this book is for its own purpose it is nevertheless a stinging indictment of the attitude of educators, and of society generally. The gifted, who might with a little extra help make a great return to society, are largely neglected; the need for prevention of the birth of the defective is largely neglected; millions of dollars are available, however, for patchwork and remedia efforts with the handicapped.

PAUL POPENOE.

A Glossary Of Genetic Terms

AGGLUTINOGEN—A substance from which an agglutinin is produced; which, in turn, is a substance which has the property of clumping and precipitating certain specific types of blood corpuscles or bacteria.

ALLELOMORPH—Mendelian characters are inherited in alternative pairs, or in alternative series. These alternative genes are called allelomorphs. Examples: Albinism (recessive), Normal pigmentation (dominant); Horns (recessive), Hornlessness (dominant).

BACK-CROSS—Cross of a hybrid to one of the parental forms.

CHIASMA—"In the diptolene stage (of cell division) the chromatids are associated in pairs in such a way that in one part of their length two chromatids are associated but in another part each is associated with a different chromatid. The point of exchange is termed a chiasma." (Sansome and Phipp, 1932.)

"Exchange of partners between the four chromatids of a bivalent." (L. H. Hill, 1932.)

CHROMATID—Chromosomes frequently bear the foreshadowing of a future longitudinal division so that they appear to be made up of two parallel threads. These threads are the chromatids.

CHROMOSOMES—Tiny dark-staining bodies visible in the nucleus of the cell at the time of cell-division. The number of chromosomes in any species is usually constant. The chromosomes carry the genes, linearly arranged, which control the development of Mendelian characters.

CROSSING OVER—Interchange of segments between two homologous chromosomes previous to the formation of gametes.

CONJUGATION—Side-by-side association of homologous chromosomes previous to formation of gametes.

DIPLOID—Having two sets of chromosomes. Body-tissues of higher plants and animals are ordinarily diploid in chromosome constitution. See *Somatic*.

DOMINANT—A character possessed by one of the parents of a hybrid, which appears in the hybrid to the exclusion of the contrasted character from the other parent (the recessive). Thus in a cross of green- and yellow-seeded peas the first generation has yellow seeds. Yellow is dominant and green is recessive, being transmitted but not appearing in the presence of the factor for yellow.

FACTOR—Same as *Gene*.

F_1—(Pronounced eff-one). The first filial generation. The offspring of a given mating.

F_2—The second filial generation. Produced by intercrossing or self-fertilizing the F_1. The inbred grandchildren of a given mating.

GAMETE—A reproductive cell of either sex; e. g. sperm or ovum.

GENE—(1) The unit of inheritance, which is transmitted in the germ cells, and which by interaction with the genic and cytoplasmic complex controls the development of a character. The genes are arranged linearly in the chromosomes. (2) "The physical basis of heredity"—or more figuratively, the atom of the genetic molecule.

HAPLOID—Having the reduced number of chromosomes, as in germ cells, as distinguished from the diploid or double number of chromosomes in normal somatic cells.

HETEROZYGOUS—Containing both genes of an allelomorphic pair, or two genes of an allelomorphic series. Heterozygous individuals generally resemble the individuals homozygous for the dominant character, but they transmit the recessive to half their offspring.

HOMOZYGOUS—(1) An organism formed by like germ cells; (2) An organism is said to be homozygous for a given character when all the germ cells transmit identical genes for this character. This is the most frequently used meaning of the term.

LINKAGE—Association of genes in inheritance, due to the fact that they are in the same chromosome.

MUTATION—A sudden variation in an inherited character.

ONTOGENY—The developmental history of an organism, from fertilized egg to adult individual

RECESSIVE—See *Dominant*.

SOMATIC—Referring to body tissues; having two sets of chromosomes, one set normally coming from the female parent and one from the male; as contrasted with germ cells having a single set of chromosomes.

SEGREGATION—Separation of allelomorphic genes at meiosis.

SELFED—Self-pollinated.

TRANSLOCATION—Attachment of a fragment of one chromosome to a non-homologous chromosome, resulting in a new arrangement of genes.

ZYGOTE—An organism produced by the union of two germ cells.

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